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*ON THE RELATIONSHIPS BETWEEN THE FREQUENCY FUNCTIONS OF STELLAR VELOCITIES**

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1. In the study of stellar motions, methods of analysis generally follow a procedure in which the data of observation are tested for certain simplifying assumptions, i.e., one solves for a number of parameters associated with an assumed law of motion and proceeds to compare the motions given by observation with those predicted on the basis of the assumed law. While such a process is legitimate when examining the validity of the assumed law, it becomes inadequate whenever a further application of the law is required because it makes the data conform to an analytical expression at a stage in the analysis where the observations should retain their full unbiased influence.

A case in point is the statistical problem of determining the luminosity function for a selected group of stars in the neighborhood of the sun. Here the pertinent observations give us the distributions in proper motion and radial velocity for stars between certain limits of apparent magnitude. The problem is really one of evaluating the law of tangential velocities, since this law (when combined with the distribution in proper motion) will yield the distribution in parallax by a familiar theorem in stellar statistics. Now many investigators have in effect derived this law of tangential velocities on the basis of some analytical space velocity function known to approximate the space motions of the stars in question. Thus the extensive studies of van Rhijn[1] have relied rather heavily on the space velocity function first suggested by Schwarzschild. Strömberg in a series of papers[2] in effect assumes a quasi equivalence of radial and tangential velocity distributions, a procedure which is not justified, as has been pointed out by Oort.[3] Again, the law of tangential velocities obtained by Luyten[4] is based on a Maxwellian distribution of the peculiar motions.

In view of what has been said earlier it would be preferable to obtain

the distribution of the cross motions, without assuming a particular analytical form for the space velocity function, by establishing a numerical law of tangential velocities which will then serve the purpose of deriving the desired distribution in parallax. Several attempts have been made towards the solution of this problem. A notable contribution was made by Bok.[5] Assuming the existence of a space velocity function in variant throughout the volume of space occupied by the stars under investigation, Bok considers the observed distribution in radial velocity along two axes normal to the direction of the region in which the law of tangential motion is required. By virtue of the assumed invariance of the space velocity function, these radial velocities are transposed to the region considered and there combined into a tangential velocity. The frequencies are computed by the rule of combining two independent events two at a time. The procedure presupposes that there is no correlation in radial velocity between both axes. On the basis of the ellipsoidal theory this assumption cannot be criticized since the theory is founded on the very hypothesis of independent distribution in space velocity components along three mutually perpendicular axes. However, a most general space velocity function of the type

$$\phi(u, v, w) \neq \phi_1(u)\phi_2(v)\phi_3(w)$$

clearly does not permit such an inference. The method is restricted by this consideration but it surpasses other methods in that it does not require a prior knowledge of solar motion, thereby bringing to zero the number of analytical parameters that enter the solution.

An important advance was made by Ambarzumian,[6] who first showed that if we admit the existence of an arbitrary, invariant space velocity function, then the observed distribution of radial velocities for a group of stars lends itself to a determination of the frequency function of the space velocity components along a system of rectangular axes. Ambarzumian's analysis reduces to a minimum the assumptions regarding the space velocity function. His contribution appears to be of considerable significance although it seems to have been generally overlooked, perhaps in part because in certain cases the data on radial velocity are insufficient for a justifiable application of the method.

We shall show how Ambarzumian's attack can be directed towards a determination of the frequency function of the cosmic or space velocities themselves for stars of known velocity along the line of sight. On the basis of this result we shall then obtain an expression for the corresponding frequency function of the tangential velocities. Again we make the only assumption mentioned before, namely that the space velocity function is constant throughout the volume of space occupied by the stars to be analyzed.

2. In what follows we shall make use of a type of function not generally encountered in the literature. Let ρ denote the absolute value of the radial velocity not necessarily corrected for solar motion. We then define $g(\rho)$ as the average frequency distribution function of the absolute values of the radial velocities over the entire sky. It is to be understood that this function is obtained by averaging the frequency distributions tabulated for equal standard areas and that it is derived from the observations directly. Thus galactic concentration or any uneven surface distribution, if present, is removed in the process of evaluating $g(\rho)$. In particular the function g must satisfy

$$\int_0^\infty g(\rho)d\rho = 1.$$

In a similar way we define $F(V)$, where V is the linear space velocity, as the frequency distribution function of the linear space velocities over the entire sky. Of course these space velocities are to be considered as referred to whatever standard of rest is adopted for the radial velocities. Again we require

$$\int_0^\infty F(V)dV = 1.$$

Let $f(\vec{V})$ denote the arbitrary (vectorial) space velocity function with respect to any set of rectangular axes. Isolate a single vector of magnitude V_i. This vector will generate over the surface of the celestial sphere a distribution in radial velocities $g_{\vec{V}_i}(\rho)$. Evidently the orientation of this vector is immaterial. Consequently any number of vectors of magnitude V_i may be conceived as evenly distributed over the surface of a sphere of radius V_i as far as their contribution to $g_{V_i}(\rho)$ is concerned. Thus for the purpose of evaluating $g(\rho)$ for all $V \geqslant \rho$, the space velocity function $f(\vec{V})$ is equivalent to an isotropic density distribution

$$D(V) = \frac{F(V)}{4\pi V^2}$$

in velocity space.

We can now set up an equation relating $g(\rho)$ to $F(V)$ and we have (see Fig. 1)

$$g(\rho)d\rho = \frac{2}{4\pi}\int\int\int \frac{F(V)}{V^2}\,d\tau,$$

where $d\tau$ is the volume element in velocity space and the region of integration extends throughout the volume between two parallel planes normal to the direction of ρ (which is arbitrary) and separated by an amount $d\rho$. The factor 2 arises because we consider absolute values of the radial velocity.

Let $d\tilde{\omega}$ denote the surface element in the plane ABC. Then

$$g(\rho)d\rho = \frac{1}{2\pi}d\rho \int\int \frac{F(V)}{V^2}\, d\tilde{\omega},$$

where the region of integration extends over the entire surface of the plane normal to ρ. Let (r, α) represent the polar coördinates of a point in this plane, measured with respect to any set of axes with origin at A. Then

$$g(\rho) = \frac{1}{2\pi}\int_0^\infty \int_0^{2\pi} \frac{F(V)}{V^2}\, r\, dr\, d\alpha$$

$$= \int_0^\infty \frac{F(V)}{V^2}\, r\, dr.$$

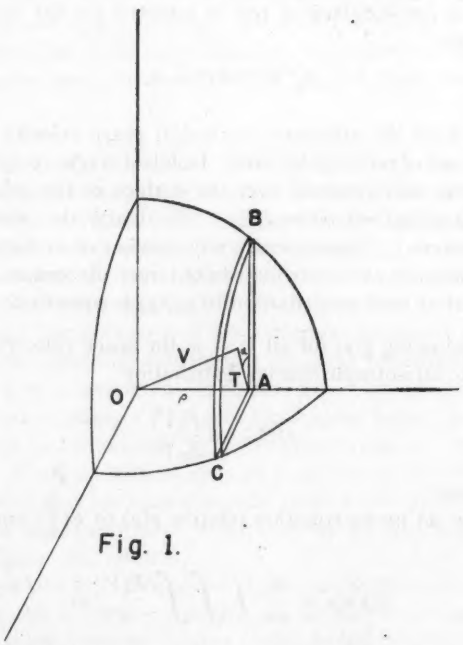

Fig. 1.

But $r^2 = V^2 - \rho^2$ and so, for given ρ

$$g(\rho) = \int_\rho^\infty \frac{F(V)}{V}\, dV. \qquad (1)$$

We take the integral to be uniformly convergent by assuming $\lim_{V\to 0} \frac{F(V)}{V} = 0$.

The solution of (1) is then given by

$$F(V) = \left[-\rho \frac{d}{d\rho} g(\rho) \right]_{\rho = V}.$$

Everything on the right-hand side of this equation is known from observation and therefore the function F is determined.

3. Let $G(T)$ denote the average frequency distribution function of the tangential velocities over the entire sky. We require

$$\int_0^\infty G(T)dT = 1.$$

As before we may conceive of the space velocity function as an isotropic density distribution in velocity space. We now have

$$G(T)dT = \frac{2}{4\pi} \int\int\int \frac{F(V)}{V^2} d\tau,$$

where the region of integration extends throughout the volume between two cylindrical surfaces with axis along ρ and separated by an amount dT. The integration is again elementary and so we readily obtain

$$G(T) = T \int_T^\infty \frac{F(V)}{V\sqrt{V^2 - T^2}} dV. \tag{2}$$

In terms of the observed function $g(\rho)$ this result may be written

$$G(T) = -T \int_0^\infty \frac{g'(\sqrt{T^2 + \rho^2})}{\sqrt{T^2 + \rho^2}} d\rho. \tag{3}$$

4. Equations (1) and (3) express the solution of the problem.[7] Inasmuch as these results are valid for a most general invariant space velocity function, we may treat as special cases those investigations of space and tangential motions based on a particular form of an invariant space velocity function.

Thus in the case of a Gaussian frequency distribution in radial velocities in any part of the sky, we have

$$g(\rho) = \frac{2}{\sigma\sqrt{2\pi}} e^{-\rho^2/2\sigma^2},$$

where σ is the dispersion in the space velocities. Here, by equation (1)

$$F(V) = \left[-\rho \frac{d}{d\rho} \frac{2}{\sigma\sqrt{2\pi}} e^{-\rho^2/2\sigma^2} \right]_{\rho = V}$$

$$= \frac{2V^2}{\sigma^3\sqrt{2\pi}} e^{-V^2/2\sigma^2}$$

in conformity with the law of chaotic velocities. The corresponding frequency distribution in tangential velocities is given by equation (2)

$$G(T) = \frac{2T}{\sigma^3\sqrt{2\pi}} \int_T^\infty \frac{Ve^{-V^2/2\sigma^2}}{\sqrt{V^2 - T^2}} dV.$$

Putting $x^2 = V^2 - T^2$ this becomes

$$G(T) = \frac{2T}{\sigma^3\sqrt{2\pi}} e^{-T^2/2\sigma^2} \int_0^\infty e^{-x^2/2\sigma^2} dx$$

or

$$G(T) = \frac{T}{\sigma^2} e^{-T^2/2\sigma^2}.$$

A case of axial symmetry in the frequency distribution of space velocities is that of a single drift superposed on a Maxwellian distribution with respect to the local standard of rest. In the usual notation, we have

$$g(\rho) = \frac{1}{4\pi} \int_0^{2\pi} \int_0^\pi \frac{2}{\sigma\sqrt{2\pi}} e^{-(\rho - V_\odot \cos\lambda)^2/2\sigma^2} \sin\lambda \, d\lambda \, d\varphi,$$

where λ is the angular distance from the antapex and φ is the variable in longitude. Integration with respect to this latter variable is immediate and so

$$g(\rho) = \frac{1}{\sigma\sqrt{2\pi}} \int_0^\pi e^{-(\rho - V_\odot \cos\lambda)^2/2\sigma^2} \sin\lambda \, d\lambda.$$

The frequency distribution of the space velocities is given by

$$F(V) = \frac{V}{\sigma^3\sqrt{2\pi}} \int_0^\pi (V - V_\odot \cos\lambda) e^{-(V - V_\odot \cos\lambda)^2/2\sigma^2} \sin\lambda \, d\lambda.$$

Let $x = V - V_\odot \cos\lambda$ and the above expression becomes

$$F(V) = \frac{V}{\sigma^3 V_\odot \sqrt{2\pi}} \int_{V - V_\odot}^{V + V_\odot} xe^{-X^2/2\sigma^2} dx$$

or

$$F(V) = \frac{V}{\sigma V_\odot \sqrt{2\pi}} [e^{-(V - V_\odot)^2/2\sigma^2} - e^{-(V + V_\odot)^2/2\sigma^2}].$$

The corresponding frequency distribution in tangential velocities is given by

$$G(T) = \frac{T}{\sigma V_\odot \sqrt{2\pi}} \int_T^\infty \frac{e^{-(V - V_\odot)^2/2\sigma^2} - e^{-(V + V_\odot)^2/2\sigma^2}}{\sqrt{V^2 - T^2}} dV.$$

Let $x^2 = V^2 - T^2$ then

$$G(T) = \frac{Te^{-T^2/2\sigma^2}}{\sigma V_\odot \sqrt{2\pi}} \int_0^\infty e^{-(V_\odot^2 + X^2)/2\sigma^2} \left(\frac{e^{V_\odot \sqrt{x^2 + T^2}/\sigma^2} - e^{-V_\odot \sqrt{x^2 + T^2}/\sigma^2}}{\sqrt{x^2 + T^2}} \right) dx.$$

By expanding the exponential functions of terms involving $V_\odot$ the above expression can be written

$$G(T) = \frac{2Te^{-T^2/2\sigma^2}}{\sigma V_\odot \sqrt{2\pi}} \int_0^\infty e^{-x^2/2\sigma^2} \left[\frac{V_\odot}{\sigma^2} + \frac{V_\odot^3}{3!\sigma^6} (x^2 + T^2) + \right.$$

$$\left. \frac{V_\odot^5}{5!\sigma^{10}} (x^2 + T^2)^2 + \ldots - \frac{V_\odot^3}{1!2\sigma^4} + \frac{V_\odot^5}{2!2^2\sigma^6} - \frac{V_\odot^5}{1!3!2\sigma^8} (x^2 + T^2) + \ldots \right] dx.$$

After term-by-term integration and some regrouping, we have

$$G(T) = \frac{Te^{-T^2/2\sigma^2}}{\sigma^2} \left[1 + \frac{V_\odot^2}{3!\sigma^2} \left(1 + \frac{T^2}{\sigma^2} \right) - \frac{V_\odot^2}{1!2\sigma^2} + \right.$$

$$\left. \frac{V_\odot^4}{5!\sigma^4} \left(1.3 + 2.1 \frac{T^2}{\sigma^2} + \frac{T^4}{\sigma^4} \right) - \frac{V_\odot^4}{3!2\sigma^4} \left(1 - \frac{3!2}{2!2^2} + \frac{T^2}{\sigma^2} \right) + \ldots \right].$$

This may be put in the form

$$G(T) = \frac{Te^{-T^2/2\sigma^2}}{\sigma^2} \sum_0^\infty A_j \left(\frac{T}{\sigma} \right)^{2j},$$

where

$$A_j = \frac{\left(\frac{V_\odot}{\sigma} \right)^{2j}}{(2j + 1)!} \left[1 - \frac{j + 1}{1!(2j + 3)} \left(\frac{V_\odot}{\sigma} \right)^2 + \right.$$

$$\left. \frac{(j + 1)(j + 2)}{2!(2j + 3)(2j + 5)} \left(\frac{V_\odot}{\sigma} \right)^4 - \ldots \right].$$

This result is identical with that obtained by Luyten.[8]

5. It can be shown that the assumed invariance of the space velocity function implies that $g(\rho)$ is a monotonically decreasing function. Hence, should equations (1) and (3) lead to negative or non-real frequencies for certain intervals in space velocity, it should be taken as an indication that within this interval the space velocity function is not invariant throughout the volume of space under investigation. In practice, a small local stream or "moving cluster," which contributes heavily to the distribution of radial velocities in a few areas of limited size, while being absent or relatively weak for the remainder of the sky, might produce peculiar distortions in the shape of $g(\rho)$. Obviously known members of local streams should be discarded in the analysis. The invariance of the frequency function of the space velocities is basic to our argument.

After our analysis had been completed, a recent paper by Colacevich[9] was received. Formulae similar to those derived here are developed but the space velocity function is assumed to be spherically symmetrical. Colacevich's work may therefore be considered as a special case of our own investigation, since we did not find it necessary to make any assumptions beyond that of the invariance of the frequency function of the space velocities.

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[1] *Groningen Publ.*, **34** (1923) and **38** (1925).

[2] *Mt. Wilson Contr.*, **395**, 93 (1930), *et seq.*

[3] *Bull. Astr. Neth.*, **239**, 289 (1932).

[4] These PROCEEDINGS, **11**, 87 (1925); Harvard Reprint No.16.

[5] *Harv. Circ.*, **400** (1935).

[6] *Monthly Notices R.A.S.*, **96**, 172 (1936).

[7] These relations can be deduced without recourse to geometry. Thus, if all stars form a single drift of velocity V_1, we observe at an angle θ from the direction of the drift a radial velocity

$$\rho = V_1 \cos\theta \tag{1a}$$

and a tangential velocity

$$T = V_1 \sin\theta. \tag{1b}$$

Giving equal weight to equal solid angles (i.e., equal areas in the sky), the probability distribution of θ in the half-sphere in which $\cos\theta$ is positive is

$$dw = d\cos\theta = \sin\theta\, d\theta. \tag{2}$$

The probability distributions of ρ and T are then found by simple substitution of (1a) and (1b) in (2):

$$g(\rho)d\rho = dw = \frac{1}{V}d\rho \tag{3a}$$

$$G(T)dT = dw = \frac{T}{V\sqrt{V^2 - T^2}}dT. \tag{3b}$$

If now the distribution of space velocities over the entire sky is given by $F(V)$, we obtain by summing (3a) and (3b) over all possible V's:

$$g(\rho) = \int_{\rho}^{\infty} \frac{F(V)}{V}\, dV$$

$$G(T) = T \int_{T}^{\infty} \frac{F(V)}{V\sqrt{V^2 - T^2}}\, dV.$$

[8] *Loc. cit.*

[9] *Publ. della Oss. Astr. di Arcetri*, Fasc. No. 64 (1948), p. 3

AMINO ACID CONSTITUENTS OF TISSUES AND ISOLATED CHROMOSOMES OF DROSOPHILA

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Introduction.—The chemical constitution of the chromosomes has been intensively studied ever since Miescher[1] discovered nucleic acid and extracted a protamine from salmon sperm. Pollister and Mirsky[2] characterize salmine (salmon sperm protamine) as lacking of tryptophane and tyrosine, and having a 31.6 per cent nitrogen content of which arginine makes up 89.2 per cent. Kossel[3] prepared a protein which he called histone from nucleated erythrocytes. Histones are proteins distinguished for possessing basic properties, and according to Mirsky and Ris[4] contain relatively little tryptophane. By enzymatic digestion and ultra-violet absorption measurements Caspersson[5] established the presence of nucleic acid and protein in the salivary gland chromosomes of Diptera, whose significance was first demonstrated by Painter[6] and Heitz and Bauer.[7] Caspersson's findings were confirmed and extended by Mazia and Jaeger[8] and Mazia,[9] who considered the continuous protein framework of a chromosome to be composed of histone, but Kossel,[3] the foremost investigator of histones, believed that only nuclei of certain kinds of tissues contained histones. *Chromosin* was extracted from various cells by Mirsky and Pollister.[10] This substance can be divided into a soluble histone fraction, and a non-histone fraction which contains tryptophane. From lymphocytes of calf thymus, Mirsky and Ris[4] isolated residual chromosomes, which were composed of arginine, cystine, tyrosine and tryptophane. In addition to the basic proteins, histone or protamine, Stedman and Stedman[11] isolated a second protein which was designated as *chromosomin*. Analysis

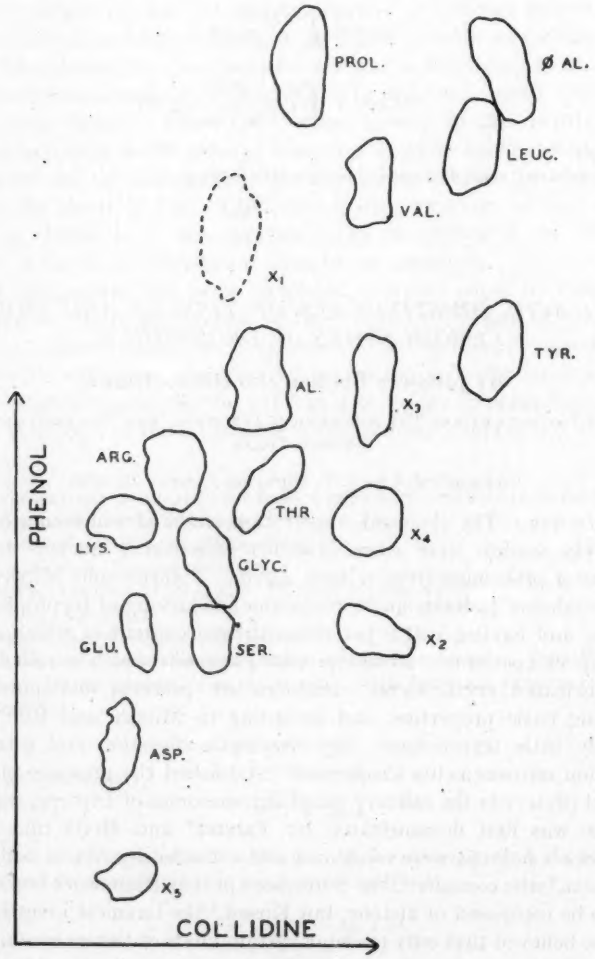

FIGURE 1

Tracing of a two-dimensional paper chromatogram of 36-hour hydrochloric acid digest of giant salivary gland chromosomes. X_1, X_2, X_3, X_4, and X_5 are as yet unidentified substances. X_1 is present in the brain tissue and is shown here to give its relative position on the chromatogram.

of chromosomin showed the presence of arginine, histidine, lysine, glutamic acid, tryptophane and cystine.

The similarity of viruses and genes may be of significance in view of the chemical and microbiological results obtained by Knight[12] on eight strains of tobacco mosaic virus. He suggests that in some cases in mutation among tobacco mosaic viruses there may be a stepwise change in amino acid content. Muller[13] states that chemically the gene is of nucleoprotein nature and that viruses are composed of "*nothing but* nucleoproteins." As viruses fulfil the definition of a gene this lends support to the idea "that the most primitive forms of life consisted of nothing else than a gene."

With the introduction by Consden, Gordon and Martin[14] of a comparatively simple technique for the detection of amino acids in very small amounts of material, the field of protein chemistry has taken on new aspects. One of the important biological applications of protein chemistry is in determining the exact nature of genetic material. This recent development of partition chromatography for identification of amino acids suggested this method of analysis. The Williams and Kirby[15] modification of this technique has been used in these experiments.

Experimental.—Various kinds of tissues of *Drosophila virilis* were utilized for these experiments. The semen including sperm was obtained from several hundred adult males. Several tissues from mature larvae were also separated for analysis. These included brains, male gonads and salivary glands. In addition, chromosomes were mechanically isolated from salivary gland cells using a squash technique. This was done by staining in acetocarmine, breaking the cells and nuclear membrane by gently tapping a cover slip, washing the chromosomes in 45 per cent acetic acid, then picking up isolated chromosomes with a micropipette. As a control on the effect of staining, whole salivary glands were stained and tested. The tissues were hydrolyzed in 3 *N* hydrochloric acid for 36 hours at 100°C. After hydrolysis, the hydrochloric acid was removed by evaporation at a low temperature under reduced pressure. The residue was taken up in a small amount of water, 0.100 ml. for the sperm and chromosomes, and 0.200 ml. for the salivary glands, brains and gonads. An aliquot of this, 0.050 to 0.100 ml., was used to prepare two-dimensional chromatograms. Phenol was used as the first solvent followed by collidine.

Figure 1 is a tracing of a chromatogram showing the amino acids which were present in the salivary gland hydrolyzate. Several spots reacting to give a typical purple color with ninhydrin were observed which do not correspond to any of the amino acid known to occur naturally. Some of these have been observed by other workers, but differences in conditions during the preparation of the chromatograms are such that comparisons with earlier observations cannot easily be made.

Table 1 shows the amino acid composition of salivary glands, chromo-

somes, brains, male gonads and sperm. X_1, which is present in the brain tissue, has been noted by us in a variety of other materials, and seems to be widely distributed. X_3 and X_5 have also been observed elsewhere. It is probable that some or all of these are amino acids yet to be identified.

The same amino acids were present in the stained as in the unstained salivary glands with the exception of X_4. Its absence may be due to the action of the stain on this compound. Otherwise no difference could be detected between the stained and unstained glands on a qualitative nor quantitative scale. The sensitivity of the ninhydrin reaction is such that if arginine were present in the hydrolyzates it should have appeared on the chromatograms. On the other hand, amino acids such as histidine, tyrosine, phenylalanine and proline, may have been

TABLE 1

AMINO ACIDS	SALIVARY GLANDS UNTREATED	SALIVARY GLANDS STAINED	CHROMOSOMES ISOLATED	BRAINS	MALE GONADS	SPERM AND SEMEN
Aspartic	+	+	+	+	+	...
Glutamic	+	+	+	+	+	...
Serine	+	+	...	+	+	...
Glycine	+	+	+	...	+	+
Lysine	+	+	...	+	+	...
Threonine	+	+	...	+	+	...
Alanine	+	+	+	+	+	+
Arginine	+	+	...	...	...	...
Valine	+	+	+	+	+	+
Leucine	+	+	+	+	+	+
Tyrosine	+	+	...	+	+	...
Phenylalanine	+	+	...	+	+	...
Proline	+	+	+	+	+	...
X_1	...	...	...	+	...	...
X_2	+	+	...	...	...	...
X_3	+	+	...	+	+	...
X_4	+	...	...	...	...	...
X_5	+	+	...	...	...	...

present in the hydrolyzates and were not revealed in the chromatograms because of the low sensitivity of the reaction of these amino acids with ninhydrin. Cystine and tryptophane would be destroyed during acid hydrolysis.

Discussion.—Stanley[16] in discussing viruses has pointed out that viruses in contrast to sperm nucleoproteins apparently do not have an excess of basic amino acids. Since certain properties of viruses have been compared with those of the gene it is therefore of interest to note that of the seven amino acids found in isolated chromosomes, valine, leucine, glutamic acid and glycine were present in all the virus strains tested by Knight.[12] Aspartic acid, alanine and proline were also present in all virus strains tested except the CV3 strain.

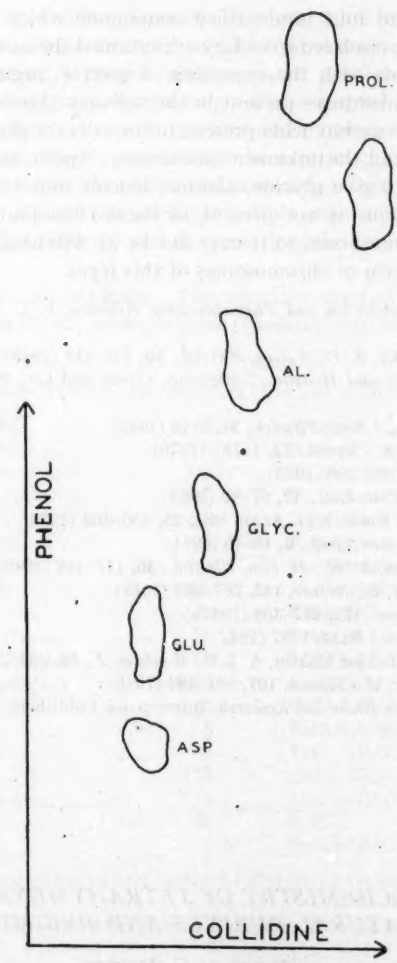

FIGURE 2

Tracing of a two-dimensional paper chromatogram of isolated chromosomes.

In this work aspartic acid, glutamic acid, glycine, alanine, valine, leucine and proline have been demonstrated in the hydrolyzate of chromosomes isolated from the giant salivary gland nuclei of *D. virilis* using the ascending paper chromatography microtechnique. The whole salivary gland contained these additional amino acids: serine, lysine, threonine, arginine,

tyrosine, phenylalanine and four unidentified coupounds which give the ninhydrin reaction. Brains isolated from larvae contained the same amino acids as the salivary glands with the exception of glycine, arginine and three of the unidentified substances present in the salivary glands. Male gonads contained all of the amino acids present in the salivary glands with the exception of arginine and the unknown substances. Sperm and semen from adult males reacted to give glycine, alanine, leucine and valine. It should be noted that arginine is not present in these Drosophila testes, sperm and semen, or chromosomes, so it may not be an essential part of the protein material of sperm or chromosomes of this form.

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*STUDIES ON THE BIOCHEMISTRY OF TETRAHYMENA. XIV. THE ACTIVITY OF NATURAL PURINES AND PYRIMIDINES**

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The requirement for purines and pyrimidines by *Tetrahymena geleii* was earlier demonstrated.[1] These requirements could be met by the addition of nucleic acid to the medium. At the time these studies were made it was necessary to add a crude extract from natural sources to supply the "Factor II" activity and this crude extract always contained some purine and

pyrimidine activity. Recently, however, it has been found that the Factor II requirement can be met by a highly active concentrate of a new vitamin-like substance, protogen[2] and increased pyridoxine, copper and iron,[3] so that the crude concentrate originally employed can be omitted. With a medium entirely devoid of purines and pyrimidines it has been possible to reinvestigate their requirements in precise quantitative and qualitative terms, and to test the activity of numerous analogs as replacers, sparers and inhibitors. This communication deals with natural purines and pyrimidines[4] in their effects upon the growth of the animal microorganism, Tetrahymena.

Material and Methods.—The organism used in these investigations was *T. geleii* strain W, grown in pure (bacteria-free) culture. The base medium

TABLE 1

BASE MEDIUM (ALL AMOUNTS GIVEN IN γ/ML. OF FINAL MEDIUM)

L-arginine HCl	83	Dextrose	2500
L-histidine HCl	36	Sodium acetate	1000
DL-isoleucine	113	Ca pantothenate	0.10
L-leucine	147	Nicotinamide	0.10
L-lysine HCl	116	Thiamine HCl	1.00
DL-methionine	94	Riboflavin	0.10
L-phenylalanine	70	Pteroylglutamic acid	0.01
DL-threonine	138	Biotin (free acid)	0.0005
L-tryptophane	28	Choline Cl	1.00
DL-valine	76	Protogen*	0.375
DL-serine	157	$MgSO_4 \cdot 7H_2O$	100.00
L-glutamic acid	233	K_2HPO_4	100.00
L-aspartic acid	61	$CaCl_2 \cdot 2H_2O$	50.00
Glycine	5	$Fe(NH_4)_2(SO_4)_2 \cdot 6H_2O$	25.00
DL-alanine	55	$FeCl_3 \cdot 6H_2O$	1.25
L-proline	175	$CuCl_2 \cdot 2H_2O$	5.00
L-hydroxyproline	75	$MnCl_2 \cdot 4H_2O$	0.05
L-tyrosine	67	$ZnCl_2$	0.05
L-cysteine	3.5	Tween 85†	700.00

* Furnished by the Lederle Research Laboratories through the courtesy of Dr. E. L. R. Stokstad.

† Furnished by the Atlas Powder Company, Wilmington, Delaware.

employed is given in table 1. Growth responses were measured turbidimetrically as previously described.[5] In all cases dose response experiments were conducted over wide ranges of concentrations of the material being tested and the experiments were repeated varying numbers of times. The results are all based on third serial transplants which, within any given experiment, were run in triplicate.

Results.—Dose response experiments were conducted to test the response of the organism to hydrolyzed yeast nucleic acid. Optimum growth was obtained upon the addition of 70 γ/ml. of final medium (Fig. 1). The ef-

fects of the various constituents of nucleic acid were then tested to determine the optimum levels of each free base and the nucleosides and nucleotides, in so far as they were available for testing.

Purines.—It was earlier shown[1] that guanine was by far the most active of the purines tested. The results we have obtained in this series of in-

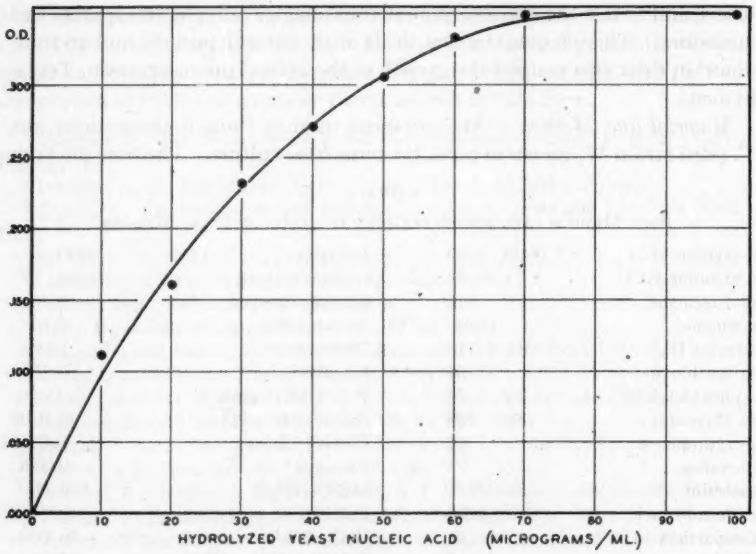

FIGURE 1

Dose response curve to alkaline hydrolyzed yeast nucleic acid.

TABLE 2

COMPARISON OF ACTIVITIES OF GUANINE, GUANOSINE AND GUANYLIC ACID. FIGURES REPRESENT THE AMOUNTS REQUIRED TO PRODUCE HALF-MAXIMUM GROWTH

	WEIGHT (γ/ML.)	MOLARITY (μM)
Guanine	8.5	50.0
Guanosine	7.5	23.7
Guanylic acid	9.0	22.5
Guanylic acid + adenine (25 γ/ml.)	3.5	8.8
Guanylic acid + adenylic (25 γ/ml.)	3.5	8.8

vestigations indicate clearly that Tetrahymena is entirely incapable of guanine synthesis and this purine must be present in the diet in order that growth may occur. Moreover, contrary to our earlier conclusions which were based on a single concentration, the free base is approximately one-half as active as either guanosine or guanylic acid on a molar basis (table 2). Guanylic acid is slightly more active, on a molar basis, than the nucleoside

(Fig. 2). In accordance with these findings guanylic acid is the preferred source of guanine for work of this kind due to its greater solubility and also because maximum yields are consistently somewhat higher.

Adenylic acid supported slight growth when used with the crude Factor II preparation.[1] This may have been due to a slight guanine contamination in the sample of adenylic acid then used (adenine was without activity) together with the small amount of guanine in the Factor II preparation. In the present medium no growth results in the absence of guanine (or its nucleoside or nucleotide) over wide ranges of concentration of either ade-

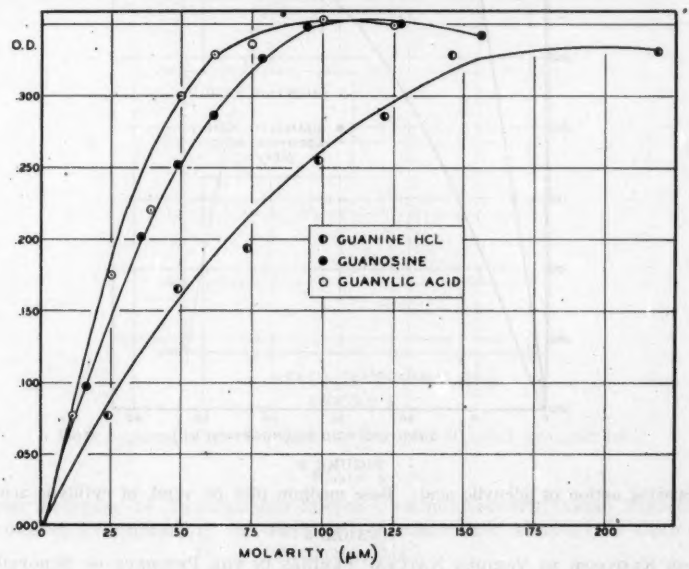

FIGURE 2

Dose response, calculated on a molar basis, to guanine, guanosine and guanylic acid. Base medium plus 50 γ/ml. of cytidylic acid.

nine or adenylic acid. Adenine can be synthesized from guanine but the reverse is not true for Tetrahymena. Both adenine and adenylic acid spare guanine, however, when added to the medium. Thus the addition of 25 γ/ml. of either adenine or adenylic acid reduces the requirement for guanylic acid for approximately half-maximum growth from 9 γ/ml. (22.5 μM) to 3.5 γ/ml. (8.8 μM) (table 2). Maximum yields are similar, however, whether adenine is synthesized by the organism or supplied in the medium (Fig. 3).

Xanthine, hypoxanthine and uric acid were tested for replacement and

sparing of guanine. Xanthine appeared to replace guanine but only at extremely high levels (1000 γ/ml.). Growth was very slow and the yields a fraction of maximum. We believe that there is every indication here of slight contamination with guanine of the xanthine used. When tested with suboptimal levels of guanylic acid (10 γ/ml.) there was some sparing action,

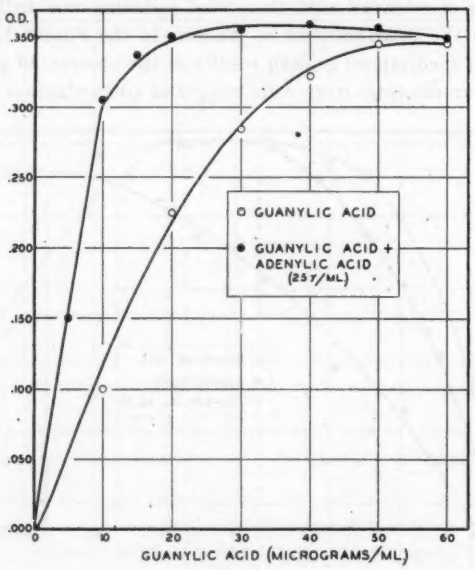

FIGURE 3

Sparing action of adenylic acid. Base medium plus 50 γ/ml. of cytidylic acid.

TABLE 3

DOSE RESPONSE TO VARIOUS NATURAL PURINES IN THE PRESENCE OF SUBOPTIMAL AMOUNTS (10 γ/ML.) OF GUANYLIC ACID

AMOUNT ADDED (γ/ML.)	OPTICAL DENSITY		
	XANTHINE	HYPOXANTHINE	URIC ACID
0	0.262	0.269	0.205
50	0.270	0.360	0.200
100	0.289	0.351	0.208
150	0.334	0.355	0.206
200	0.359	0.354	0.211
250	0.376	0.344	0.219

but again the high concentrations required would indicate a guanine contamination (table 3).‡ Neither hypoxanthine nor uric acid supported growth in the absence of guanine. Uric acid appears to be entirely inert and without either inhibitory or sparing action (table 3). Hypoxanthine, on the other hand, was active in sparing guanylic acid. The addition of 50 γ/ml.

of hypoxanthine together with suboptimal amounts (10 γ/ml.) of guanylic acid raised the growth to the normal maximum level. A comparison of the activities of hypoxanthine, xanthine and uric acid are shown in table 3.

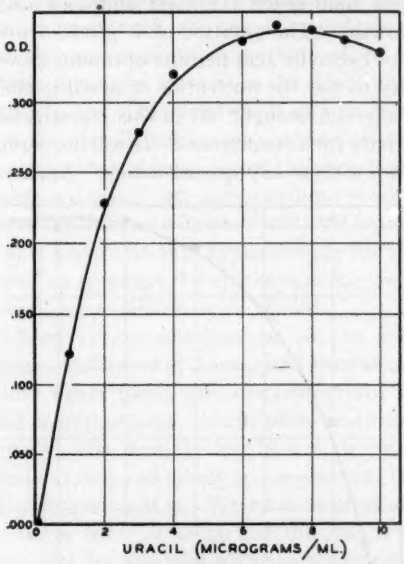

FIGURE 4

Dose response to uracil. Base medium plus 50 γ/ml. guanylic acid.

TABLE 4

DOSE RESPONSE TO THYMINE AND 2-METHYL-5-ETHOXYMETHYL-6-AMINO PYRIMIDINE (THIAMINE PYRIMIDINE) IN THE PRESENCE OF SUBOPTIMAL AMOUNTS OF CYTIDYLIC ACID (10 γ/ML.)

AMOUNT ADDED (γ/ML.)	OPTICAL DENSITY	
	THYMINE	THIAMINE PYRIMIDINE
0	0.220	0.231
100	0.225	0.229
200	0.252	0.206
300	0.264	0.199
400	0.271	0.189
500	0.280	0.184
600	0.301	0.175
700	0.293	0.163
800	0.268	0.154
900	0.265	0.149
1000	0.286	0.150

Pyrimidines.—No growth of Tetrahymena occurs when the medium is free of pyrimidines. The addition of either uracil or cytidylic acid produces

normal growth responses. Uracil is more active on a weight basis (1.5 γ/ml. for approximately half-maximum growth) than cytidylic acid (4.5 γ/ml. for half-maximum growth). On a molar basis, however, cytidylic acid is slightly more active than uracil (12.5 μM and 13.4 μM, respectively, for half-maximum growth). The addition of 7 γ/ml. of uracil (Fig. 4) or of 20 γ/ml. (Fig. 5) of cytidylic acid permits optimum growth. We have not had an opportunity to test the nucleotide of uracil in the present medium.

A most interesting fact brought out in this investigation was that cytosine is without activity for Tetrahymena. It will not serve as a replacement for cytidylic acid nor is there any sparing action. Apparently the organism

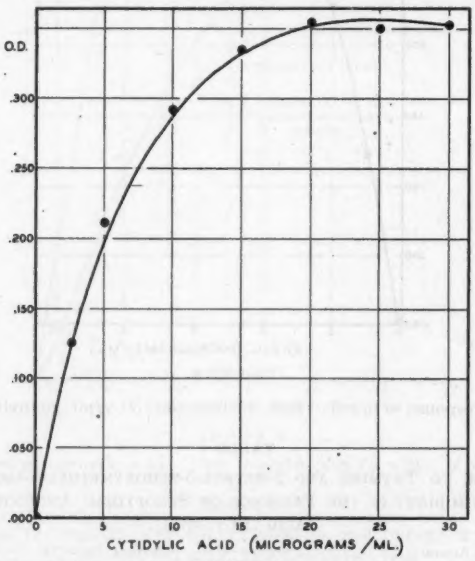

FIGURE 5

Dose response to cytidylic acid. Base medium plus 50 γ/ml. guanylic acid.

cannot metabolize this free base but can readily metabolize uracil. Similarly thymine is without activity for replacement and shows such weak sparing power as to indicate a slight chemical contamination of the sample tested (table 4).§

A test on the pyrimidine of thiamine (2-methyl-5-ethoxymethyl-6-amino pyrimidine) demonstrated that it is not able to replace uracil in the medium and becomes slightly inhibitory at high concentrations (table 4).

Discussion.—The failure of Tetrahymena to synthesize guanine from adenine and its undoubted ability to accomplish the reverse reaction contrasts this animal with higher forms in this one respect. Brown, *et al.*,[6] showed

that when N^{15} labeled adenine was administered to rats the heavy nitrogen appeared in the guanine of the nucleic acids, while labeled guanine was not incorporated into the nucleic acids. It seems probable that of the enzyme systems for the interconversion of adenine and guanine, which were present in the animal prototypes, the enzyme catalyzing the synthesis of adenine was lost in the mammalian (and perhaps other) lines and that catalyzing the synthesis of guanine was lost in the ciliate line.

The nearly equal activity of the nucleoside and nucleotide indicates the relative difficulty of the riboside linkage as compared with phosphorylation.

As brought out earlier the evidence favors the view that this organism is incapable of utilizing xanthine, but hypoxanthine spares guanine. This may mean that hypoxanthine, with its unsubstituted 2-position, can be converted to adenine or it may mean that hypoxanthine has some other definite function in the organism (perhaps the synthesis of inosinic acid). No data from the present work are available on this point.

The similarities between our observations on the pyrimidine requirements of Tetrahymena and those of Loring and Pierce[7] on Neurospora are striking. Loring and Pierce found that certain mutant strains would not grow in the absence of pyrimidines. Nucleosides and nucleotides of uracil were many times more active than the free base while cytosine was entirely inactive for one strain (1298) and nearly so for a second (H263). Cytidine and cytidylic acid were very active. We have not had an opportunity to test cytidine, uridine or uridylic acid§ but the results with cytosine as opposed to cytidylic acid are identical with the above on Neurospora.

It appears that Tetrahymena is able to accomplish the linkage between the base, uracil and the sugar to form the riboside but cannot do so when the base is cytosine or thymine. It may be that the enzyme catalyzing the production of riboside is so constituted that it will act only at the uracil surface and the amino group in the 6-position of cytosine or the methyl group in the 5-position of thymine block its function. It must be true, however, that thymine nucleotide and cytidylic acid are synthesized when the sole pyrimidine source is uracil, and that uracil and thymine nucleotides must be formed when the only source of pyrimidine is cytidylic acid. This would indicate that Tetrahymena possesses the necessary enzymes to methylate the 5-position without breaking the nucleotide down to the free base, and to substitute the amino for the keto group in the 6-position without breaking the pyrimidine-to-sugar linkage.

Summary.—The animal microorganism, Tetrahymena, requires an exogenous source of purine and pyrimidine for growth. None of the natural purines tested, except guanine, would support growth. Guanylic acid was slightly more active than guanosine and twice as active as guanine on a molar basis. Adenine, adenylic acid and hyoxanthine spare guanine, while uric acid is without activity. Xanthine possessed low sparing activity at

high concentrations but this can probably be attributed to a slight chemical contamination of the sample used.

Uracil or cytidylic acid can serve as the pyrimidine source for Tetrahymena while cytosine and thymine cannot. Cytidylic acid and uracil are nearly equal in activities on a molar basis. Neither cytosine nor thymine possesses sparing action. Thiamine pyrimidine (2-methyl, 5-ethoxymethyl, 6-amino pyrimidine) is slightly inhibitory at high levels.

* Supported by a grant from the U. S. Public Health Service and a grant recommended by the Committee on Growth acting for the American Cancer Society.

‡ Since this paper went to press a sample of synthetic xanthine was prepared for us by Dr. George H. Hitchings. This compound exhibited no guanine activity.

§ Since the above was written we have had the opportunity to test the following compounds: diammonium uridylate (prepared in the laboratory of H. S. Loring); cytidine (from the Levene collection); thymidine (sent to us by Dr. E. L. R. Stokstad). The uridylate and the cytosine exhibited the same activity, on a molar basis, as cytidylic acid. The thymidine was inactive. The range of concentrations of thymidine tested, however, was extremely limited due to the small amount of the compound available.

[1] Kidder, G. W., and Dewey, V. C., *Arch. Biochem.*, **8** 293 (1945).

[2] Stokstad, E. L. R., Hoffman, C. E., Rezan, M. A., Fordham, D., and Jukes, T. H., *Ibid.* (in press).

[3] Kidder, G. W., and Dewey, V. C., *Ibid.* (in press).

[4] Cytosine was obtained through the courtesy of Dr. George H. Hitchings of the Wellcome Research Laboratory; thiamine pyrimidine was obtained through the courtesy of G. W. Lewis of Merck Research Laboratories, while all of the other purines and pyrimidines were obtained from commercial sources.

[5] Kidder, G. W., and Dewey, V. C., PROC. NAT. ACAD. SCI., **34**, 81 (1948).

[6] Brown, G. B., Roll, P. M., and Plentl, A. A., *Federation Proc.*, **6**, 517 (1947).

[7] Loring, H. S., Pierce, J. G., *J. Biol. Chem.*, **153**, 61 (1944).

ON LEAF ARRANGEMENT IN METASEQUOIA GLYPTOSTROBOIDES

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Communicated by R. W. Chaney, October 1, 1948

Recently I had occasion to aid Dr. Ralph W. Chaney of this institution in arriving at a more exact understanding of the phyllotaxy of *Metasequoia glyptostroboides* Hu and Cheng, and the results of this investigation seem worthy of recording.

It has already been pointed out that the leaves of *M. glyptostroboides* are arranged decussately,[1] and indeed this is quite plain in some parts of the plant; however, modifications of this arrangement occur which make a more detailed statement of value.

The material examined includes a series of herbarium specimens from eastern Szechuan and northwestern Hupeh, China, collected by C. T. Hwa; seedlings grown by N. T. Mirov, of the California Forest and Range Experiment Station from seeds collected on the Hsieh expedition of 1947; and young trees and staminate spikes collected by R. W. Chaney in March, 1948.

The shoots of *M. glyptostroboides* are of two kinds, "long" shoots in which growth is usually indeterminate, and "short" shoots with usually determinate growth; the latter are deciduous as units. Long shoots can start growth as short ones, and vice versa. Conceivably, shoots of an intermediate nature may be found, although so far I have seen none.

The long shoots, as in other plants with shoot dimorphism, are found at the ends of the more rapidly growing branches and at the tip of the vertical axis. On the vertical axis there is little tendency for the leaves to become distichous by rearrangement, and it is here that the decussate phyllotaxy is most apparent (Fig. 1, × 1). On the lateral branches, in young trees and presumably at the tops of older ones, the decussate arrangement may still be obvious near the vertical axis where the square stem of the lateral branch is oriented horizontally and vertically, as seen in cross-section. But a few inches from the vertical axis the stem gradually twists to assume a position position of about 45° from the horizontal, and the leaf pairs bend on their bases toward the horizontal, thus more or less approaching a two-ranked condition. Here there may be found some twisting of the stem between nodes such as will be described under the short shoot, but only a very slight twist has been observed.

The short shoots are borne in the axils of the leaves of the long shoots (Fig. 2, × 1/2), and also in leaf axils of short shoots in many cases. They usually come to lie more or less parallel with the ground, as do the mature leaves of the shoot. Frequently short shoots will continue growth, branch, and may start growth as long shoots. Branching short shoots apparently may be the only means of growth in some of the slower growing branches; further examination of specimens taken during the growing season from mature trees is necessary to ascertain this point satisfactorily. Most often the leaves of short shoots are much more closely spaced than those of the long, but sometimes a short shoot will grow rapidly with widely spaced leaves. In such cases the most reliable means of distinguishing between the two shoots is by comparing their growing terminal buds, which, with their subtending leaves, have quite characteristic forms. Also, those of the long shoots (Fig. 1) often have a darker, more blue-green color than those of the short shoots (Figs. 3 and 4, × 1).

Leaves of the short shoots are also decussately arranged, but it is only in the terminal bud that this arrangement is unmodified. Figure 5 (× 35) is a camera lucida drawing of a cross-section of such a terminal bud, made at the

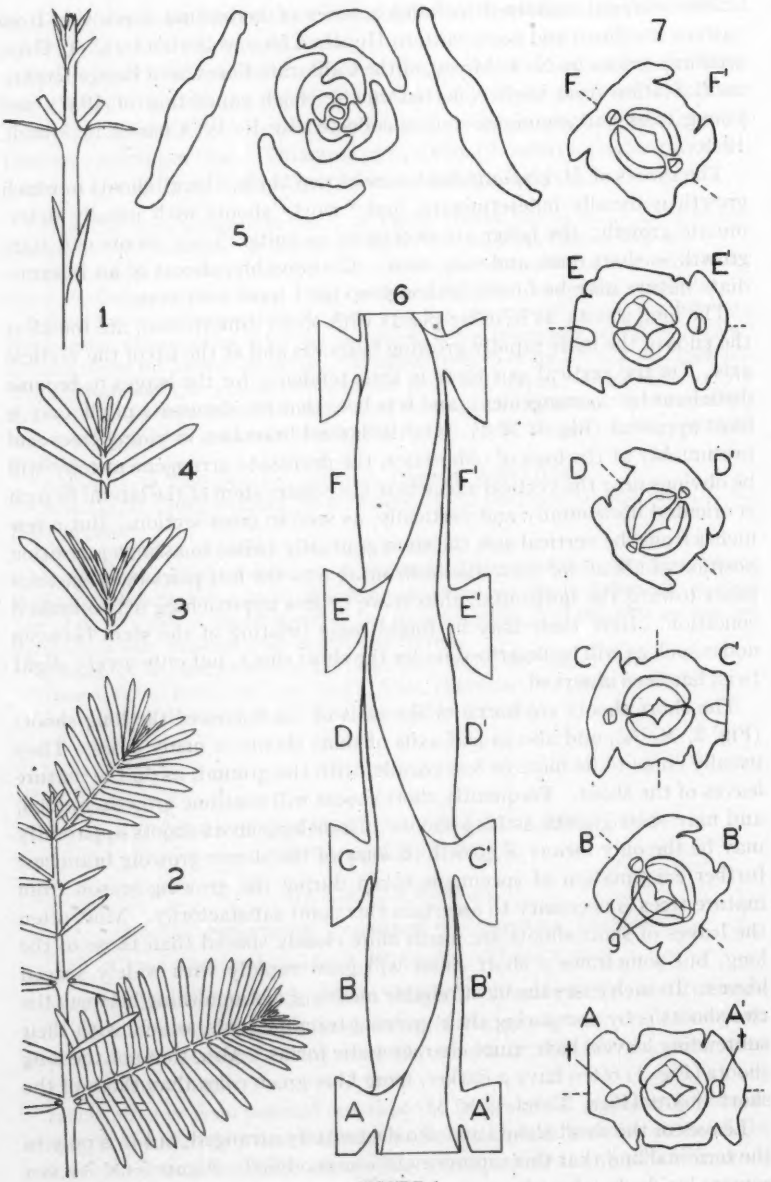

FIGURE 1

level of the apical meristem. Here are seen six pairs of leaf primordia, five of them in regular decussate arrangement. However, as each successive leaf pair enlarges and opens outward from the bud, its node twists so as to bring the leaf bases into a plane approximately parallel with the ground. "Node" is here used to indicate only the attachment point of the leaf blade, disregarding the decurrent base. The change from non-twisted to twisted internodes is usually quite abrupt: there is no twist between the nodes of the fifth and sixth primordia shown here, and there is a 75° twist between nodes of leaves six and seven. The turning of the leaf pairs is evidently dependent on their attaining a certain size, when the force produced by the acting stimulus is sufficient to bring about a turning. The nature of the stimulus is not certain; it seems likely that light is the primary factor. Application of the force is apparently at the nodes, as would be expected. Alternating nodes rotate respectively clockwise and counterclockwise, bringing all the leaf bases into the same plane with an angular twist of slightly less than 90° between any two nodes.

When the bud is growing vigorously (Fig. 3) one pair of enlarging leaves closely follows another, and as one starts to turn toward the plane of the mature leaves in one direction, the next is apparently already exerting some force in the opposite direction; this results in the terminal bud remaining oriented at about 45° from the leaf plane, as seen in end view. However, when growth has slowed down considerably (Fig. 4), one pair of leaves may enlarge and turn before the next has reached an appreciable size, and in this event the whole bud will turn as the leaf pair turns, there being no opposing force. When this happens the next oldest leaf pair is automatically brought at right angles to the leaf plane, and when it in turn opens outward, its node will rotate in the opposite direction, bringing the following leaf pair to a right angle position, and so on. In either case the effect on the stem is the same.

In order to illustrate the twisted nature of the stem, figure 6 has been drawn to show diagrammatically an enlarged segment of the mature stem of a short shoot, and in figure 7 (× 21) are shown camera lucida drawings of stem sections (material from C. T. Hwa, collection no. 179) taken from positions corresponding to those indicated in figure 6. The sections are shown as seen from the tip of the shoot looking toward the base and are taken in that order; the dotted line indicates the level of the stem as seen in *A–A′*.

In section *A–A′* the two leaf traces (*t*) are seen as they have just entered the cortex, and the shape of the pith indicates that the leaf gaps (*g*) extend as grooves in the xylem above the points of actual junction of the traces. In *B–B′* the position of the leaf traces and gaps indicates that the whole stem is twisted at a 45° angle. One leaf trace has already joined the vascular cylinder, and the other is about to join it. The rather frequent

occurrence of leaves which are not quite opposite one another at the node is probably of little significance; in some such cases the leaf traces join the vascular cylinder unequally and in others they do not. Section *C–C'* completes the 90° twist; the traces of *A–A'* are fully fused with the vascular cylinder and those of *C–C'* have entered the cortex. Again the leaf gaps of the traces of *A–A'* are seen to extend as grooves, this time below the fusion points of the traces. The groove extensions of the leaf gaps give anatomical evidence of the decussate phyllotaxy, since where grooves of adjacent nodes overlap, those of one node are always 90° apart from those of the next. *D–D'* and *E–E'* show the same procedure occurring, this time in the reverse direction, and therefore there is no continuous spiral. *F–F'* illustrates the twist starting again clockwise as in *B–B'*.

The amount of twist between nodes may vary greatly from one shoot to another; in one very young tree the variation was from almost no twist in some to a full 90° twist in others. Even in the same shoot the amount of twist varies considerably, apparently at random. In one observed case circumstances had produced a 100° twist between two nodes. The average seems to be roughly 75°. Differences in amount of twist are compensated for by a bending of each leaf on its base toward the horizontal, so that all short shoots appear flat-ranked. However, in the older short shoots which have continued growth and increased considerably in diameter, there is frequently a reorientation of the leaves on their bases away from the horizontal plane, so that the position of the leaf indicates more nearly the position of the leaf base. This gives the appearance of the stem's untwisting, but it is very doubtful if such a thing occurs.

The twisted stem so typical of the short shoot is also found in the majority of cases in the spike bearing the staminate strobili. Again there is a great deal of variation in the amount of twist between nodes, and some spikes show almost none. Investigation shows the internal situation to be much the same as in the short shoot, the traces from the leaves subtending the strobili and the leaf gaps following the same pattern.

The shoots bearing the ovulate strobili in most instances show little or no twisting between nodes. Details have not been investigated but it seems reasonable to assume that where twisting is present the behavior of traces and gaps will be essentially the same as in the short shoot.

No attempt has been made here to compare *M. glyptostroboides* with other apparently related genera, such an undertaking being beyond the scope of this paper. It is hoped that these facts may help in leading to a better understanding of the nature and relationships of this interesting tree.

[1] Stebbins, G. L., Jr., *Science*, 108 (2796), 95–98 (1948); Hu, H.-H., and Cheng, W.-C., *Bull. Fan Mem. Inst. Biol.*, N. Ser., 1 (2), 153–161 (1948).

AN ASCENT OF KOROYANITU

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Communicated by E. D. Merrill, October 4, 1948

Koroyanitu is the high point of the Mt. Evans Range, a high and narrow ridge rising from the grassland hills of northwestern Viti Levu. This largest island of the Fijian archipelago is physiographically separable into two parts by a central mountain axis dominated by the Rairaimatuku Plateau, an extensive forested area with an average elevation of perhaps 800–900 meters. The western half of Viti Levu and a strip along the north coast are relatively dry savanna and bush, locally known as the *talasinga* country. The eastern half is wet forested land, called by the natives the *veikau*. The line of demarcation between these two types of land is often well defined. The Mt. Evans Range lies entirely within the dry zone of Viti Levu, but in height it is third on the island, exceeded only by Tomanivi, near the northern edge of the Rairaimatuku Plateau, and Korombasambasanga, south of the plateau. Because of its altitude (1195 meters), the Mt. Evans Range receives a heavy rainfall on its upper slopes and is well forested above an approximate 700 meters. Isolated from the main forest of Viti Levu by many miles of low, broken, reed-covered *talasinga*, the forested upper slopes of the Mt. Evans Range offer a tempting goal to a botanist. This range was selected as my first objective during a recent botanical reconnaissance of Fiji in 1947–1948.[1]

The Mt. Evans Range had the further advantage, in the eyes of a botanical explorer, of being essentially unknown botanically,[2] although it had been explored by some of the surveyors who in recent years have provided the Lands and Survey Department, of Suva, with excellent detailed maps of the larger islands.

As headquarters for my five-week reconnaissance of the Mt. Evans Range, the Fijian village of Nalotawa was selected. Nalotawa lies at the eastern base of the Mt. Evans Range and has an elevation of about 550 meters, being situated in a wooded valley in the grassland, but only a mile or two from the beginning of the forest on the slopes of the range. On a prearranged day about 15 Fijian "boys" from Nalotawa met me and my "head assistant," a capable young Fijian named Tanieli Rawangga, at a sugarcane plantation in the valley of the Mba River, to which point we had brought our supplies by truck. The professional tropical plant collector cannot travel light; he must have a supply of collecting paper, blotting-paper driers, corrugated boards, presses, straps, stoves and kerosene for drying specimens, axes, machetes, sundry other tools, and staple food supplies for whatever period he plans to remain in "the bush." My 15 carriers

were loaded with 30 or 40 pounds each when we finally left the road. In making contact with village people and in arranging for carriers it is quite essential, in a country like Fiji, to work through the chiefs and to have the proper official introductions. Throughout my work in that Crown Colony I have enjoyed the kindest coöperation from British officials and from Fijians of all classes, from "Rokos" and "Mbulis" (the principal provincial and district chiefs) to the simplest villagers.

Our route led westward from the Mba River over gently rolling grassy hills for a few miles, and then upward with increasing precipitousness along the sharp lower spurs of the Mt. Evans Range. These sharply dissected lower slopes are covered with mixed grasses; in northwestern Viti Levu an introduced grass, *Pennisetum polystachyon*, has taken control of vast areas and has swamped the native vegetation. It is a tall grass, forming dense stands two meters or more in height, and its leaves and slender inflorescences encroach upon the trail, giving one the impression that one is struggling through an endless wheat field, but a wheat field as nearly vertical as horizontal. The trail follows the crests of ever-steepening spurs, from which one looks down startling slopes to the little bush-filled valleys far below. After about ten miles of arduous walking, we came abruptly to the crest of a ridge and saw below us, among mango and orange trees, the houses of Nalotawa.

The remaining hours of our first day were spent in a continuous pow-wow with all the adult male members of the community, in the large and excellently built native house of Tui Yakete, the ranking chief of a group of five adjacent villages. From time to time we were served *yanggona* in the ceremonial Fijian manner; this beverage, the *kava* of the Polynesians, is prepared from the root of *Piper methystichum* and is consumed on every plausible occasion by the Fijians. No business transaction can be carried on, no arrival heralded, no departure consummated, without recourse to the *yanggona* bowl and its attendant rigid ceremony. Coming at length to the point, Tanieli explained my work to the villagers and presented my official credentials; Tui Yakete reciprocated by turning over to us his house as living and working quarters, assigning men to work with us in the field, and promising to supply us with staple native foods. Finally I was able to seek my sleeping mat, but this evening—and most evenings, as I learned—many villagers stayed in the house after I retired and continued their conversation quite uninhibited, from time to time dozing on the mats. It is considered impolite in Fiji to terminate a visit abruptly.

For the first few days I collected on the slopes of the range, following the same route higher each time. The route selected for our ascent of the range lay over the saddle of a massive eastern outlier, which itself is dominated by a huge pinnacle of bare rock known as Nairosa or "The Thumb." From the base of the actual pinnacle, which has an elevation of more than 1000 meters, we were able to obtain excellent views over the countryside and to plan

our further route. This followed a narrow ridge to the eastern flank of the main range itself. Several of my willing assistants spent a day cutting a rough track through the dense vegetation of this ridge. Directly below the main peak of Koroyanitu they located a fairly level spot on the ridge, not far from a tiny stream, cleared a small camp-site and set up a canvas fly.

I usually planned to have four or five Fijians accompany me on field trips, as this many helpers are desirable in a forested country where cutting of tree specimens is a frequent necessity; tropical woody specimens are so bulky that, if several duplicate sets are obtained, a quantity of material needing several men to carry is the result of a good day's work. When the day arrived for our ascent of Koroyanitu, however, ten boys of the village presented themselves. Although the peak is not distant from the village, only one of these boys had previously ascended it, and he had been a surveyor's carrier many years before. With this considerable retinue of ten local boys and Tanieli, carrying collecting supplies and food for a couple of days, I left Nalotawa on May 1 to put "operation Koroyanitu" into effect. We were accompanied by numerous hunting dogs, in case we should locate a wild pig. On an earlier day this hunting pack had had a brush with a wild pig with rather unsatisfactory results from a canine point of view, one dog being completely eliminated and another being lost for three days in the *veikau*, finally finding his way home badly crippled. One has to admire the temerity of these Fijian hunters, who track down and kill often dangerous wild pigs with no other weapon but a metal pike.

We entered the forest on the slope of Nairosa and proceeded along the now familiar lower part of the trail. It was a fine day, but even so the forest was dark and gloomy, as the sun does not penetrate to the ground through the dense canopy of the trees. Underfoot were boulders of all shapes and sizes, and the wet clayey soil, so characteristic of the Fijian hills, made the walking difficult as the slope gradually steepened. Soon the spectacular peak of Nairosa towered above us, discernible through occasional breaks in the foliage. Passing through the saddle below this pinnacle, we emerged on the long curving ridge and followed it westward. Our route was now more level but even more difficult underfoot, as the vegetation of the exposed ridge was windswept and tangled, interlaced with scrambling ferns and the branches of a sprawling *Freycinetia*.

Soon after noon we had crossed the diminutive stream which represents the "highest water" on this slope, and ten minutes' climb above this I found the camp-site which my advance party had selected; indeed they had located the only even approximately level spot in the vicinity. Here we had lunch and rested. After a while I set some of the boys to work extending our minute clearing, others to cutting a trail toward the summit, and took a couple with me to collect in the immediate vicinity. From our camp-site we could not see Koroyanitu, but a frontal and slightly lower peak, Koro-

ynasamama, towered above us; it is Fijian custom to give each peak a separate name, but actually I could not ascertain that the natives had any name for the entire range which Europeans in the vicinity call the Mt. Evans Range. The vegetation near our camp was of upland crest type, with gnarled and dwarfed trees jammed together in a dense moss-cloaked forest. Few individual trees in such a habitat exceed six or eight meters in height; only on the sheltered slopes of ridges, or in deep wet valleys, do individual trees attain a larger size. The components of this upland forest are exceedingly varied and so mixed that no species can be considered dominant. Of frequent occurrence among the trees, however, were two conifers, probably *Podocarpus* spp.,[3] a small-leaved *Alphitonia*, and species of such genera as *Alstonia*, *Hedycarya*, *Tapeinosperma*, *Aglaia*, *Elaeocarpus*, *Dolicholobium*, etc. Several undershrubs of the beautiful genus *Cyrtandra* bore attractive white flowers, as did various species of the ubiquitous genus *Psychotria*. The whole mass of woody vegetation, at this altitude, is interlaced with lianas of the genera *Medinilla*, *Maesa*, *Agatea*, and *Morinda*, and quantities of epiphytic orchids, ferns and small cryptogams cover the wet branches and the vegetation-debris underfoot. Several hours of diligent collecting gave us a fair sample of the vegetation surrounding our camp, and at the end of that time we were all ready to enjoy our supper of yams, *ndalo* (*Colocasia*), tinned meat and tea. The members of my crew left at the camp-site had occupied themselves to good purpose, making rough shelters for themselves and even clearing a "line" through the tangled forest to give us a perfect view of the pinnacle of Nairosa, with which we were now on a level. This concession to scenic appreciation I particularly approved at dawn the next morning, when the rising sun outlined the black pinnacle against a red sky, setting up for me a kodachrome picture which serves to remind me that on rare occasions, at least, it can be a pleasure to arise at dawn.

We were indeed fortunate to have a second clear morning, for in the Fijian mountains one cannot expect two consecutive days without rain. Even on clear days the clouds gather quickly on the summits, and so one's only hope of good visibility from the peaks is to reach them early in the day. Starting from our camp-site immediately after a quick breakfast of yams, *ndalo*, and tea, we followed the trail which our advance guard had slashed the preceding afternoon. This final ascent was a bitterly steep and rough climb among roots and huge boulders, winding around the base of Koroynasamama, and finally up a precipitous cliff, to emerge suddenly from the impeding tangle of vegetation onto the summit ridge. Although it is difficult, from below, to pick out the high point of the Mt. Evans Range, one has no doubts when standing on Koroyanitu, for this knife-edged crest emerges from the jumble of ridges and clearly overtops its neighboring peaks. We took turns standing upon the high point, which is a conglomerate boulder about two meters in diameter. The view from this vantage point, on our

remarkably clear morning, was spectacular. To the west we looked down on the Viti Levu coast and the town of Lautoka, while the entire Yasawa chain of islands was spread before us, lying hazily on the blue sea, dwarfed by distance and made insignificant by our height. To the south the mass of the Mt. Evans Range impeded much of the view, but the distant Koromba,[4] green with its summit forest, stood above the yellowed and sharply eroded grassland hills. To the east lies Nairosa, now well below us, and the mass of Viti Levu, its rough undecipherable topography leveling off in the distant Rairaimatuku Plateau; on this day even Tomanivi was briefly visible, but soon it was engulfed by the cloud mass which so often lies upon the central plateau. By ten o'clock the visibility had dwindled to the immediate foreground, and the rest of the day was intermittently foggy and cloudy.

The summit ridge of Koroyanitu proved to be a collector's dream, and for a long time I could only put into the press as rapidly as possible the offerings brought by my interested and observant boys, who now knew that I wanted ten duplicates of each flowering or fruiting plant. Eventually we worked southward on the ridge for a mile or so, collecting carefully as far down the steep slopes as was consistent with safety. At noon we made a clearing from which we could observe the nearby summit of Mbotilamu, and here we had our lunch of yams, *ndalo*, tinned fish, and tea. The vegetation of the summit was superficially similar to that of the camp-site, but many different species were observed and collected. Noteworthy were four distinct species of *Piper* (the genus which provides *yanggona*), and on the highest boulder I was pleased to observe a plant of *Medinilla longicymosa*, the beautiful pink-bracted melastome which occurs only on Viti Levu, and there only on a few of the higher peaks. A locally common fern is *Oleandra Parksii*, most unfernlike in appearance, with its erect rhizomes forming stiff thickets a meter high and its fronds simulating the leaves of an angiosperm.

When we had returned to the camp-site it was three o'clock, and a storm was rapidly gathering. As I contemplated the prospect of spending a wet night on this exposed spot and the difficulties of returning down a wet trail, I suggested to the boys that we break camp and make a quick return to the village before dark, if possible. This necessitated a conference of all hands, in which the pros and cons were carefully discussed, regardless of the moments slipping by. The ayes won out, and so the camp was folded up and the remaining yams and *ndalo*, which had thoughtfully been cooked at breakfast time, were eaten (for it would have been foolish to carry them back to the village, and improvident to abandon them). At length we departed, slithering down the wretched path, among the gloomy trees, around the dark boulders and massive roots, at a definitely good pace. The decision was a fortunate one, for hardly had we reached the edge of the forest before we were caught in the advancing storm. The last part of the descent, in semidarkness over the rain-soaked grassy trail, brought us to Nalotawa

before total darkness. Clouds enveloped the mountain throughout the night and the next day, and we had no cause to regret our precipitate retreat. Mountain camps in the rain are scarcely enjoyable, and one develops an appreciation of the comparative comforts of native villages.

After such a profitable trip as that described above, I had to spend two or three long days working in the village, making notes and preparing, pressing and drying the specimens. Such days were pleasantly spent, as a good Fijian house makes a fine headquarters, and one is assured of congenial company. When I had finished my work in the evening, many of the villagers would come to visit and we would sit on the mats drinking *yanggona* and conversing, by way of Tanieli as my interpreter. Fijians are tireless conversationalists, and one hears, every evening, a steady hum ascending from the village houses. But they are definitely unacquainted with the spirit of Shakespeare's lines which Proust uses to introduce his great novel:

"When to the sessions of sweet silent thought
I summon up remembrance of things past, . . ."

The foregoing episode, covering a few days in the life of a plant taxonomist, may serve to acquaint the reader with the first step in a phytogeographical problem. In most tropical countries we are still in the "alpha" phase of plant classification, when the flora is so imperfectly known that novelties may be expected and gaps in the distributional data are obvious. During the nine months which I spent in Fiji in 1947–1948, some 26,000 herbarium specimens were collected and prepared, these representing upward of 2900 field numbers. The first set of material has been deposited in the herbarium of the Arnold Arboretum, and the nine duplicate sets will be sent to some of the other large world herbaria. Supplementary material consisting of 226 wood samples and flowers and fruits in preservative was also acquired.

What is the purpose of such collections? The unattainable goal of systematic botanists is to record the distribution of all plants and to classify them in a system which will, in some manner, depict their phylogenetic history. The primary purpose of our great herbaria is thus to present a picture, by means of representative specimens, of the composition of the modern plant world. These herbaria must be the chief basis for future monographic and phytogeographical studies. But they also serve many others beside the taxonomist; the economic botanist, the ethnobotanist, the morphologist, the geneticist, and students of many other disciplines seek much of their basic data in the collections and publications of systematic botanists.

[1] The mentioned botanical excursion, of which this paper briefly details a single episode, was made by the writer under the auspices of the Arnold Arboretum of Harvard University and was largely financed by a John Simon Guggenheim Memorial Foundation Fellowship. Generous financial support was also received from the BACHE FUND

of the NATIONAL ACADEMY OF SCIENCES and the Penrose Fund of the American Philosophical Society. To these organizations the writer is deeply grateful.

[3] Mr. William Greenwood, a resident of Lautoka, Viti Levu, and an enthusiastic amateur botanist, has made several excursions to the western slopes of the Mt. Evans Range and has ascended the subsidiary southernmost peak, Mbotilamu, which is only slightly lower than Koroyanitu. As a result of Mr. Greenwood's excellent collections, which in recent years have been sent to the Arnold Arboretum for study, several new species of flowering plants were discovered on and near the Mt. Evans Range, including *Elatostema Greenwoodii*, *Dysoxylum pilosum*, *Pterocymbium oceanicum* and *Tapeinosperma Greenwoodii*. The unusual features of Mr. Greenwood's collections first called the writer's attention to this neglected area and gave it priority when the opportunity to pursue field work was offered.

[3] Although representative specimens were obtained from all the plants mentioned, their exact botanical identification must await detailed study of the entire collection.

[4] Pickering Peak of the Europeans, and the second isolated forested range of western Viti Levu. An ascent of this was subsequently made by the writer; it is somewhat lower than Koroyanitu, but is more isolated and offers a more difficult climb.

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*NUTRITIONAL LIFE HISTORY AS INFLUENCED BY DIETARY ENRICHMENTS. III. FULL-LIFE DATA OF 1946–1948 EXPERIMENTS**

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In previous papers of this series[1, 2] we have reported that starting with a basal diet of natural foods containing 14.4 per cent of protein and 0.2 per cent of calcium, with laboratory-bred rats as experimental animals, supplementation with meat protein results in more rapid growth and earlier reproduction, but occasionally at some cost to stability. Usually but not always there has been spontaneous recovery.

Such experiments have now been extended to larger numbers; and, in the cases started earliest, to the completion of the life histories.

Table 1 summarizes the average findings for all of the completed full-life studies with the two diets chiefly used in our earliest-started experiments. Comparing the first two columns of figures in this table it will be seen that the larger numbers of findings fully confirm our previous report of more rapid growth and earlier puberty in the animals receiving the protein supplement. These animals also reared somewhat more and larger young Their distinctly lesser average age at death is doubtless due to the greater incidence of premature deaths in early adulthood.

The last 3 columns of table 1 give the average finding of 5 comparisons of litter mates receiving, respectively (1) the basal Diet A (Diet 16) alone

(2) Diet 16 P 5 consisting of Diet 16 plus a supplement of 5 g. of meat six days each week, and (3) Diet 16 P 10 containing twice as large a meat (protein) supplement. This was a series in which no premature deaths occurred, and the lengths of life on the three diets were essentially alike. In other respects also, the two levels of meat feeding (protein supplementation) yielded practically the same results.

TABLE 1

AVERAGE RECORDS OF FEMALE RATS ON DIET 16 ALONE OR WITH PROTEIN (MEAT) SUPPLEMENT: COMPLETED LIVES

	ALL COMPARABLE CASES ON THESE TWO DIETS		FIVE CASES EACH LITTER-MATE PARALLELS		
	16 CASES ON DIET 16	19 CASES ON DIET 16 P 5	ON DIET 16	ON DIET 16 P 5	ON DIET 16 P 10
Gain in body wt., 28th–56th days of life, g.	43	60	37	62	62
Age at birth of first young, days	121	107	120	100	94
Number of young borne, per female	40	41	30	45	53
Number of young reared, per female	28	34	24	35	43
Average wt. of young at 28 days, g.	39	44	40	46	43
Age at death, days	820*	668†	846	849	905

* One of the 16 of this series died before 400 days of age.

† Four of the 19 of this series died before 400 days of age.

While the figures in table 1 are believed to give a valid general impression, they are not offered as a precise measure either of the incidence of "premature" deaths or of the effect of protein supplementation. Moreover, as pointed out in our previous papers[1, 2] the occasional unfavorable reactions are very largely prevented by increasing the calcium content of the diets receiving the extra protein. Experiments to determine the effect of such calcium supplementation are still in progress, and these with their controls will also increase the volume of data from which to judge the occasional suggestions of imbalance.

TABLE 2

EARLY GROWTH AND LENGTH OF LIFE OF MALE RATS ON DIETS 16, 16 P 5 AND 16 P 10

	10 CASES ON DIET 16	10 CASES ON DIET 16 P 5	6 CASES ON DIET 16 P 10
Gain in body wt., 28th–56th days of life, g.	49	82	78
Age at death, days	741	748	711

Table 2 summarizes the data of growth and length of life of the males corresponding to the females represented in table 1. The protein supplementation clearly increased the rate of growth in the males and to about

the same proportionate degree as in the females. The length of life was not significantly influenced in either direction. There were no "premature" deaths among the 26 male rats used in these experiments. Nor have we observed in any of these males the symptoms of excessive nervousness which occasionally appeared among the females as previously described.

* Aided by grants from the John and Mary R. Markle Foundation to Columbia University.

[1] Sherman, H. C., and Pearson, C. S., PROC. NAT. ACAD. SCI., **33**, 264–266 (1947).

[2] Sherman, H. C., and Pearson, C. S., *Ibid.*, **33**, 312–314 (1947).

ON THE PROTEINS OF a^+a^+ AND aa EPHESTIA

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It has been shown previously that lack or reduction of pigment in a number of organs in Ephestia homozygous for the gene *a* is due to lack of kynurenin, a precursor of the pigment.[1] Kynurenin is formed from tryptophane in the metabolism of a^+-animals. In *aa* moths the tryptophane content of the proteins is higher than in the wild type.[2] Since no concomitant increase in protein nitrogen was found, it was concluded that either a new type of protein is formed under the influence of the gene *a*, or that proteins rich in tryptophane replaced others poor in tryptophane. In either case, the protein make-up of the cell would be changed.

Since proteins perform important functions in the cell, it should be expected that other characters of the cell are also changed. Actually it has been found that fat content,[2, 3] viability,[4] speed of development[4] and possibly O_2 consumption of homogenates[5] are reduced in *aa* animals. It has been concluded that as a result of the mutation $a^+ \rightarrow a$ the biochemical make-up of the cell is changed in several respects.

The characters influenced by the genes a^+ and *a* are summarized in table 1. Included in this table are the effects of a third allele a^k as far as they are known. Besides differing in a number of pigmentation characters, a^+ and *a* differ from each other in chemical composition (kynurenin content, tryptophane content, fat content), and in some general biological characteristics such as viability and speed of development. The gene a^k appears intermediate between a^+ and *a*, as far as pigmentation characters are concerned. The same appears to be true for kynurenin content, since a^ka^k mothers were able to pass on a substance capable of darkening larval ocelli to their a^ka offspring, and since the same maternal effect was observed in *aa*

offspring from *aa* mothers into which degenerating $a^k a^k$ ovaries had been grafted.[6] The speed of development, on the other hand, is still more reduced in $a^k a^k$ than in *aa*. With regard to pigmentation characters and kynurenin formation, the series of genes would be $a^+ > a^k > a$, while with regard to speed of development they would be arranged in the order $a^+ > a > a^k$. Similar differences in serial arrangement in multiple alleles according to the characters observed have been repeatedly found. The remaining characters have not been investigated in $a^k a^k$.

It appears difficult to decide in which physiological order the different characters observed should be arranged. It was proved by injection experiments[1] that the pigment reduction in *aa* is due to lack of kynurenin. A

TABLE 1

PLEIOTROPIC EFFECTS OF THE GENES a^+, a^k AND a

	a^+a^+	a^ka^k	aa
A. Pigmentation characters			
1. Eyes	Black	Brown	Red
2. Brain	Brown	....	Light pink
3. Testes	Pigmented	Weakly pigmented—colorless	Colorless
4. Larval ocelli	Strong pigmentation	Intermediate pigmentation	Weak pigmentation
5. Larval hypodermis	Pigmented	Colorless	Colorless
6. Proteins	Pink	....	White
B. Chemical constitution			
7. Kynurenin	Present	Reduced in amount	Strongly reduced or absent
8. Protein tryptophane	....	?	Increased
9. Ether-extractable substances	....	?	Reduced
C. General biological characteristics			
10. Viability		Reduced	Reduced
11. Speed of development		Strongly reduced	Reduced
12. O_2 consumption in homogenates		?	Reduced ?

block of the oxidation of tryptophane to kynurenin may be considered to be the primary effect of the gene *a*. The non-oxidized tryptophane would then be stored secondarily in part in the proteins which are consequently qualitatively changed. The reduction in fat content, in viability and in speed of development may be assumed to be a consequence of the altered protein constitution. In $a^k a^k$, the amount of kynurenin seems to be smaller than in a^+-, but larger than in *aa*. The proteins of $a^k a^k$ may therefore be expected to be intermediate in tryptophane content. Unfortunately, this assumption could not be investigated. It can be imagined, however, that the resulting $a^k a^k$ proteins have a more profound action on speed of development than

the *aa* proteins. Considerations of this kind may explain the frequent occurrence of non-seriability found in multiple alleles.

An alternative assumption would be that the formation of certain proteins rich in tryptophane is the primary step caused by the gene *a*. In this case tryptophane bound up in the proteins would not be available for kynurenin formation. Again the change in fat content, etc., may be another consequence of the changed protein constitution. If the difference in protein constitution were the primary effect of the gene *a*, causing less tryptophane to be available for the formation of kynurenin, it might be expected that *aa* proteins might release tryptophane at a slower rate than a^+a^+ proteins under the influence of proteolytic enzymes. With this possibility in mind, autolysis was studied in a^+a^+ and *aa* homogenates. In the experiments, fully grown a^+a^+ and *aa* larvae were used. The *aa* strain had been crossed out previous to the experiment for 8 and 9 consecutive generations to the a^+a^+ strain used, so that the alleles were compared on a reasonably isogenic background. 2.5–3.0 g. larval material were finely ground in homogenizers according to Potter and Elvehjem in 3 ml. Ringer solution isotonic for Ephestia and buffered with 0.02 *M* phosphate buffer to pH 6.8. The larvae were homogenized at 0°C. for 10 minutes. In the homogenates, total tryptophane was determined according to the method of Sullivan and Hess,[7] and total nitrogen by a micro Kjeldahl procedure. One ml. of the homogenate was pipetted into each one of 5 small test tubes and incubated in a water bath at 31°C. The homogenate was examined for non-protein nitrogen and for non-protein tryptophane at 0, 1, 2, 4 and 6 hours after the start of the experiment. 0.1 ml. of 3 *M* trichloroacetic acid was added to each tube, and the precipitate filtered off and washed with 0.4 ml. H_2O. In the filtrate, tryptophane and nitrogen were determined. Seven paired experiments with both a^+a^+ and *aa* homogenates and one experiment using a^+a^+ material only were run.

At time 0, there are 8 measurements of tryptophane and nitrogen for a^+a^+, and 7 for *aa* which can be used to indicate the tryptophane content of a^+a^+ and *aa* larval material. The data are given in tables 2*a* and *b*. In

TABLE 2*a*

TRYPTOPHANE AND NITROGEN CONTENT IN HOMOGENATES OF ISOGENIC a^+a^+ AND *aa* EPHESTIA IN MG./G. WET WEIGHT

STRAIN	TOTAL N	NON-PROTEIN N	TOTAL TRYPTOPHANE	NON-PROTEIN TRYPTOPHANE
a^+a^+	13.8	1.49	1.22	0.04
aa	14.5	1.43	1.42	0.10

table 2*a*, the values for protein and non-protein nitrogen and tryptophane are given, expressed in relation to wet weight. Qualitatively, the data indicate an increase in total and non-protein tryptophane in *aa* as compared

to a^+a^+ without a concomitant increase in nitrogen. For a quantitative analysis, these data are unsuited because of the variability of both nitrogen and tryptophane in relation to wet weight. Quantitative data for tryptophane in relation to nitrogen content are given in table 2*b*.

TABLE 2*b*

RATIOS OF TRYPTOPHANE AND NITROGEN IN THE TOTAL AND NON-PROTEIN FRACTION OF a^+a^+ AND *aa* EPHESTIA HOMOGENATES

	a^+a^+	*aa*	*t*	$P_{df=13}$
$\frac{\text{Total tryptophane}}{\text{Total N}}$	0.088	0.098	2.251	< 0.05
$\frac{\text{Non-protein tryptophane}}{\text{Non-protein N}}$	0.027	0.070	3.241	< 0.01
$\frac{\text{Non-protein N}}{\text{Total N}}$	0.108	0.099	0.068	> 0.5
$\frac{\text{Non-protein tryptophane}}{\text{Total tryptophane}}$	0.033	0.070	3.315	< 0.01

The ratio total tryptophane/total nitrogen is increased in *aa* as compared a^+a^+. The difference is slightly below the 0.05 level of significance, i.e., just on the borderline of statistical significance. It appears, however, that this difference is real, in view of previously published results,[7] in which it has been found both for *aa* imagoes and *aa* larvae that the tryptophane content as related to dry weight is increased in comparison with a^+a^+ animals. Furthermore, the second line of table 2*b* shows that the non-protein tryptophane expressed in terms of non-protein nitrogen is higher in *aa* than a^+a^+ homogenates. This difference is well below the 0.01 level of significance. It should be pointed out that in the data involving non-protein tryptophane the level of significance calculated is probably too high, since 2 of the 8 values for a^+a^+ were given as 0, while they may have contained amounts of tryptophane too small to be measured. On the other hand, differences in the same direction and of the same order of magnitude have been found previously for *aa* and a^+a^+ imagoes, so that the conclusion appears justified that in *aa* material the amount of non-protein tryptophane is increased. No separate values for protein tryptophane are available in the present series of experiments. The tryptophane values in table 2*a*, columns 3 and 4, indicate, however, that the absolute amounts of non-protein tryptophane (0.04 and 0.10 mg./g. wet weight) are too small to account for the whole difference in total tryptophane content between a^+a^+ and *aa* material, 0.16 mg./g. wet weight. It must be concluded that part of the increased tryptophane content of *aa* is stored in the proteins, in agreement with earlier direct findings in imagoes. On the other hand, the ratio non-protein tryptophane/total tryptophane is almost twice as large

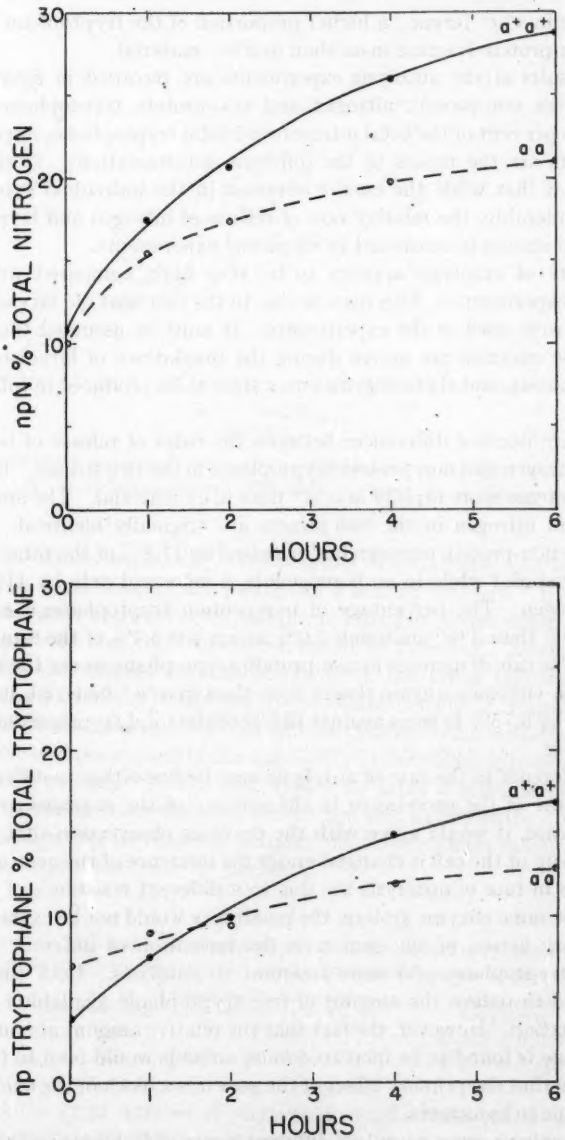

FIGURE 1

Rate of autolysis of homogenates from a^+a^+ and *aa* Ephestia: (*a*) release of non-protein nitrogen; (*b*) release of non-protein tryptophane.

in *aa* than in a^+a^+ larvae; a higher proportion of the tryptophane is found in the non-protein fraction in *aa* than in a^+a^+ material.

The results of the autolysis experiments are recorded in figure 1. In these curves non-protein nitrogen and non-protein tryptophane are expressed as per cent of the total nitrogen and total tryptophane, respectively. The points are the means of the different determinations. It should be emphasized that while the curves obtained in the individual experiments vary considerably, the relative rate of release of nitrogen and tryptophane in the two strains is consistent in all paired experiments.

The rate of autolysis appears to be very high, compared with other autolysis experiments. This may be due to the fact that old larvae nearing pupation were used in the experiments. It must be assumed that potent proteolytic enzymes are active during the breakdown of larval tissues at metamorphosis, and these enzymes may start to be produced in fully grown larvae.

There are decided differences between the rates of release of both non-protein nitrogen and non-protein tryptophane in the two strains. Both substances increase more rapidly in a^+a^+ than in *aa* material. The amounts of non-protein nitrogen in the two strains are originally identical. After 6 hours, the non-protein nitrogen has increased by 17.8% of the total nitrogen in a^+a^+ material while in *aa* homogenate it increased only by 11% of the total nitrogen. The percentage of non-protein tryptophane is originally higher in *aa* than a^+a^+ material, 7.0% as against 3.3% of the total tryptophane. The rate of increase in non-protein tryptophane under the influence of autolytic enzymes is again slower in *aa* than in a^+a^+ material, increasing in 6 hours by 6.75% in *aa* as against 13.5% of the total tryptophane in a^+a^+ homogenate.

The difference in the rate of autolysis may be due either to differences in the structure of the proteins or in the activity of the enzymes concerned. In either case, it would agree with the previous observation that the protein make-up of the cell is changed under the influence of the gene *a*. If the differences in rate of autolysis are due to a different resistance of the proteins to the same enzyme system, the possibility would not be excluded that the primary action of the gene *a* is the formation of different proteins richer in tryptophane and more resistant to autolysis. Both these facts would tend to reduce the amount of free tryptophane available for kynurenin formation. However, the fact that the relative amount of non-protein tryptophane is found to be increased in *aa* animals would tend to favor the alternative that the primary effect of the gene *a* is a block of the oxidation of tryptophane to kynurenin.

If tryptophane were bound in different types of linkage in a^+a^+ and *aa* proteins, it might possibly be released during autolysis at different rates in relation to nitrogen. Material concerning this question is given in table 3

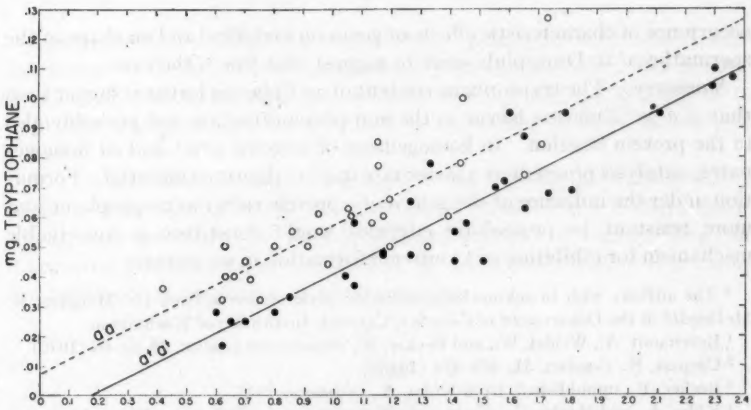

FIGURE 2

Correlation between non-protein nitrogen and non-protein tryptophane: (*a*) in a^+a^+ homogenates; (*b*) in *aa* homogenates. The lines represent the regression equations.

and figure 2. In figure 2, the corresponding tryptophane and nitrogen values for the same samples are plotted in a scatter diagram. If tryptophane were released at a faster rate, relative to nitrogen, in one strain than in the other, the slopes of the two curves would be different. Actually the slopes for the two strains are almost identical, the linear regression coefficients being 0.0496 and 0.0497 mg. tryptophane per mg. N, respectively. The closeness of the association of the different values found with the linear regression line and consequently the variability of the values is indicated by the correlation coefficient. The last values on table 3 indicate that the correlation coefficients for the two strains are not significantly different. All these findings give no reason to suspect that tryptophane is bound in a different way in *aa* than in a^+a^+ proteins.

TABLE 3

RELATION BETWEEN NON-PROTEIN NITROGEN AND NON-PROTEIN TRYPTOPHANE IN THE COURSE OF AUTOLYSIS IN a^+a^+ AND *aa* EPHESTIA HOMOGENATES

STRAIN	NO. OF DETERMINATIONS	REGRESSION COEFFICIENTS MG. TRYPTOPHANE/MG. N	CORRELATION COEFFICIENT
a^+a^+	30	0.0497	0.923 ± 0.027
aa	29	0.0496	0.817 ± 0.062

In view of the great number of physiological differences found between a^+a^+ and *aa* animals the question appears legitimate whether physiological differences of the same order of magnitude may be associated with other genes. While no direct evidence on this point is available the frequent

occurrence of characteristic effects of genes on viability[8] and on shape of the spermatheca[9] in Drosophila seem to suggest that this is the case.

Summary.—The tryptophane content of *aa* Ephestia larvae is higher than that of a^+a^+ Ephestia larvae in the non-protein fraction and probably also in the protein fraction. In homogenates of isogenic a^+a^+ and *aa* homogenates, autolysis proceeds at a faster rate in a^+a^+ than in *aa* material. Formation under the influence of the gene *a* of a protein richer in tryptophane and more resistant to proteolytic enzymes would constitute a conceivable mechanism for inhibition of kynurenin formation in *aa* animals.

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THE RAYLEIGH-RITZ AND THE WEINSTEIN METHODS FOR APPROXIMATION OF EIGENVALUES. II. DIFFERENTIAL OPERATORS

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1. In the present paper we are going to apply the results of our first paper[1] to eigenvalue problems for differential operators. In general, the problems will be of the following type. Given two linear (ordinary or partial) differential operators A and B, A of higher degree than B, the operators being defined for functions in some domain D, we consider the equation

$$Au = \theta Bu, \qquad \theta \text{ a constant parameter.} \tag{1}$$

We want then to find functions satisfying in the domain D the equation (1) and on the boundary C of D some homogeneous boundary conditions which will be denoted by (B).

The problem is to find the values of the parameter θ for which such functions $u \not\equiv 0$ exist. In the usual cases, when the problem is well defined, it will admit a discreet sequence of eigenvalues θ_k, and our aim will be to apply the results of our previous paper to the computation of these eigenvalues.

2. To this effect we have to transform the differential problem into a problem concerning a completely continuous operator in a Hilbert space. To do this we follow the already classical method of transforming the differential problem (1) into an equivalent variational problem concerning the minimum or maximum of the expression

$$\frac{\mathfrak{A}(u)}{\mathfrak{B}(u)} \tag{2}$$

for all functions u defined in the domain D and satisfying the boundary conditions (B).[2] The expressions $\mathfrak{A}(u)$ and $\mathfrak{B}(u)$ are quadratic functionals, usually integro-differential forms in the function u. They are chosen in such a way that equation (1) be the Euler equation of the variational problem. It is possible to do this only when the operators A and B are self-adjoint differential operators. In this case, for the simplest kind of boundary conditions, it is possible to take the $\mathfrak{A}$ and $\mathfrak{B}$ as given by the formulae

$$\mathfrak{A}(u) = \int_D Au \cdot u \, d\omega, \qquad \mathfrak{B}(u) = \int_D Bu \cdot u \, d\omega.$$

We will have to suppose further that the form $\mathfrak{A}(u)$ is positive definite. In many cases this form can be transformed (by use of boundary conditions) into a formally positive form, for example:

$\int_D -\Delta u \cdot u \, d\omega = \int_D [u_x^2 + u_y^2] \, d\omega$, for the boundary condition $u = 0$,

$\int_D \Delta\Delta u \cdot u \, d\omega = \int_D |\Delta u|^2 \, d\omega$, for the boundary condition $u = \dfrac{\partial u}{\partial n} = 0$.

For two differential problems, with the same equation (1) but with different boundary conditions (B) and (B'), the corresponding variational problem may deal with the same quadratic forms $\mathfrak{A}(u)$ and $\mathfrak{B}(u)$. But when the differential problems are well defined, the classes of admissible functions are different—no one being contained in the other.

3. We now translate the variational problem into language of the Hilbert space.[3] To this effect we consider the class $\mathfrak{K}$ of admissible functions, i.e., the class of functions for which the operators A and B are defined, the quadratic forms $\mathfrak{A}$ and $\mathfrak{B}$ are finite and the boundary conditions (B) are satisfied.

In this class the quadratic definite positive form $\mathfrak{A}(u)$ defines a norm

$||u|| = \sqrt{\mathfrak{A}(u)}$ and a scalar product $\mathfrak{A}(u, v)$, which we will denote as usual in the Hilbert space by (u, v).

The class $\mathfrak{K}$ does not yet form a Hilbert space because it is not complete. By a functional completion[4] we get from $\mathfrak{K}$ a class of functions $\overline{\mathfrak{K}}$ forming a Hilbert space. Usually the form $B(u)$ may be extended on the whole of $\overline{\mathfrak{K}}$ and will form there a completely continuous quadratic form (the degree of B being smaller than that of A).

By a classical theorem of Fréchet-Riesz, the quadratic form $\mathfrak{B}$ gives rise to a symmetric completely continuous operator K such that

$$\mathfrak{B}(u) = (Ku, u). \tag{3}$$

Further, we will have the equality

$$AKu = Bu \qquad \text{when } AKu \text{ exists.} \tag{4}$$

As we have already noticed, for two variational problems which differ only in the boundary conditions, say (B) and (B'), and which concern the same expression (2), the classes of admissible functions are never included one in another. In spite of this, it might very well happen that if we pass from classes $\mathfrak{K}$ and $\mathfrak{K}'$ to the complete spaces $\overline{\mathfrak{K}}$ and $\overline{\mathfrak{K}'}$, we get the inclusion $\overline{\mathfrak{K}} \subset \overline{\mathfrak{K}'}$. The explanation of this lies in the fact that some boundary conditions are stable and others unstable in respect to the operation of completion for a given quadratic form $\mathfrak{A}$. This means that some boundary conditions will remain valid for all functions of the completed class whereas others will not.

For instance, take the quadratic form $\mathfrak{A}(u) = \int |\Delta u|^2 \, d\omega$ and, as boundary conditions (B), consider $u = \Delta(u) = 0$ on the boundary C, and as boundary conditions (B'): $u = \dfrac{\partial u}{\partial n} = 0$ on C. It can be proved that when we complete the class $\mathfrak{K}$ the only remaining boundary condition will be $u = 0$, but when we complete the class $\mathfrak{K}'$, both the boundary conditions remain valid (the second, $\dfrac{\partial u}{\partial n} = 0$, in a weakened form).

As can be seen in this example, we will have in general $\overline{\mathfrak{K}} \subset \overline{\mathfrak{K}'}$, if all the boundary conditions of $\mathfrak{K}'$ which are not satisfied by $\mathfrak{K}$ are unstable.

We will now consider the eigenvalue problem for the operator K, which is of the type considered in our first paper. As before, we consider the variational problem concerning the expression

$$\frac{(Ku, u)}{(u, u)} = \frac{\mathfrak{B}(u)}{\mathfrak{A}(u)} \tag{5}$$

which is the inverse of the expression (2). Consequently, the eigenvalues

of K are the inverses of the eigenvalues of our variational problem (2). The eigenfunctions u_n will satisfy the equation

$$Ku_n = \lambda_n u_n. \tag{6}$$

In order that these eigenfunctions be solutions of our differential problem, we have to make a hypothesis which is usually satisfied, in that there exists a positive integer γ such that

$$K^\gamma u \in \mathcal{K} \quad \text{for every } u \in \overline{\mathcal{K}}, \tag{7}$$

and since we then have for u_n (by (4)), $AK^\gamma u_n = BK^{\gamma-1}u_n$: $Au_n = \theta_n Bu_n$, with $\theta_n = \dfrac{1}{\lambda_n}$, and as $K^\gamma u_n = \lambda_n^\gamma u_n \in \mathcal{K}$, u_n satisfies equation (1) and all the boundary conditions.

By making some other hypotheses which are usually satisfied in the cases which have been considered, we also prove, conversely, that every solution of the differential eigenvalue problem is an eigenfunction for our operator K with the corresponding eigenvalue $\lambda_n = \dfrac{1}{\theta_n}$.

4. The basic theorem which allows us to apply the methods of Rayleigh-Ritz and Weinstein to the differential problems is the following:

THEOREM P. *If two variational problems of type (2), with the same quadratic forms $\mathfrak{A}$ and $\mathfrak{B}$ but different classes $\mathcal{K}$ and $\mathcal{K}'$ give rise to complete spaces $\overline{\mathcal{K}}$ and $\overline{\mathcal{K}'}$ with $\overline{\mathcal{K}} \subset \overline{\mathcal{K}'}$, the operator K is the part of K' in $\overline{\mathcal{K}}$.*

This theorem shows the importance of completing the classes $\mathcal{K}$ and $\mathcal{K}'$ by functions. If we completed them by abstract elements we would not be able to compare the classes $\overline{\mathcal{K}}$ and $\overline{\mathcal{K}'}$.

We will now illustrate the application of the Weinstein and generalized Rayleigh-Ritz methods by a few examples.

We will consider, in particular, the problem of eigenvalues of a clamped plate. The differential problem is the following one:

$$\Delta^2 u = \theta u, \ \mathcal{K}: u = \frac{\partial u}{\partial n} = 0 \text{ on } C. \tag{8}$$

5. We will first apply Weinstein's method by considering another problem with the same equation but with boundary conditions given by

$$\mathcal{K}': \ u = \Delta u = 0 \text{ on } C. \tag{8'}$$

This second problem is easily seen to be equivalent to the problem of vibrations of a membrane, namely, the problem $\Delta u + \sqrt{\theta}\, u = 0$ in D, $u = 0$ on C.

The two problems lead to variational problems with the same forms $\mathfrak{A}$ and $\mathfrak{B}$, namely

$$\mathfrak{A}(u) = \int_D |\Delta u|^2 \, d\omega, \qquad \mathfrak{B}(u) = \int_D |u|^2 \, d\omega. \tag{9}$$

The complete class $\overline{\mathcal{K}'}$ is the class of all functions $u(z)$:

$$u(z) = \int_D g(z, z') f(z') \, d\omega', \tag{10}$$

where g is the ordinary Green's function of the domain D, $f = -\Delta u$ and f is in square integrable in D. The boundary condition $u = 0$ is maintained (is stable), but the condition $\Delta u = 0$ is lost (unstable). The complete class $\overline{\mathcal{K}}$ is a subclass of $\overline{\mathcal{K}'}$, and as already has been said, the condition $u = 0$ is stable and the $\dfrac{\partial u}{\partial n} = 0$ is also stable in a weakened form. The latter condition is equivalent to a condition first introduced by S. Zaremba,[5] in that $(u, p) = 0$ for all $p \in \overline{\mathcal{K}'}$ harmonic of second order (i.e., $\Delta^2 p = 0$). With $f = -\Delta u$, $h = -\Delta p$, it means $\int_D fh \, d\omega = 0$ for all h harmonic and in square integrable. If $\mathcal{P}$ is the class of all the p, it follows that $\overline{\mathcal{K}'} \ominus \overline{\mathcal{K}} = \mathcal{P}$.

We can now give the expressions for the operators K' and K. We introduce the functions

$$g_2(z, z') = \int_D g(z, z'') g(z'', z') \, d\omega'' \tag{11}$$

(the Green's function for $\Delta^2 u = 0$, $u = \Delta u = 0$ on C),

$$g_{II}(z, z') = \textit{Green's function for } \Delta^2 u = 0, \; u = \frac{\partial u}{\partial n} = 0 \text{ on } C. \tag{12}$$

As functions of z (for z' fixed), $g_2 \in \overline{\mathcal{K}'}$ and $g_{II} \in \overline{\mathcal{K}}$. We have then

$$K'u = \int_D g_2(z, z') u(z') \, d\omega', \qquad u \in \overline{\mathcal{K}'}, \tag{13}$$

$$Ku = \int_D g_{II}(z, z') u(z') \, d\omega', \qquad u \in \overline{\mathcal{K}}. \tag{14}$$

For both operators K and K', the integer γ of (7) is $= 1$ and we have

$$\text{for } u \in \overline{\mathcal{K}'}: \; K'u \in \mathcal{K}', \qquad \Delta^2 K'u = u, \tag{15}$$

$$\text{for } u \in \overline{\mathcal{K}}: \; Ku \in \mathcal{K}, \qquad \Delta^2 Ku = u. \tag{16}$$

Now, if we know the complete solution of the problem of vibrations of a membrane for a domain D, we can take the class $\overline{\mathcal{K}'}$ as the starting class for Weinstein's method and, by a choice of a sequence, $\{p_k\} \in \mathcal{P}$, we may calculate approximate values for the eigenvalues of K, i.e., the eigenvalues of the clamped plate. This is how Weinstein himself proceeded in his investigations.[6] He applied the method to the case of a rectangle where the membrane problem is explicitly solved.

But the method may be applied in a much more general case. We have only to change our starting class. Instead of changing the boundary

conditions and maintaining the same domain D, we can maintain the boundary conditions by taking a domain D_0 larger than D. This means that we will consider the problem of a clamped plate in the domain D_0. We shall have to suppose then that the domain D_0 is chosen so that we know explicitly the solutions of the clamped plate problem. For instance, we can take D_0 to be a circle. We will then consider the quadratic forms $\mathfrak{A}$ and $\mathfrak{B}$ in D_0 as well as in D, and we will consider the class $\overline{\mathcal{K}}$ for the domain D and $\overline{\mathcal{K}_0}$ for the domain D_0. If the function u of $\overline{\mathcal{K}}$ is continued in the whole domain D_0 by putting $u(z) = 0$, for $z \in D_0 - D$, it becomes a function defined in D_0 and belonging to $\overline{\mathcal{K}_0}$, as is easily proved. In this way the class $\overline{\mathcal{K}}$ may be considered as contained in $\overline{\mathcal{K}_0}$. It forms there a closed linear subspace and for the functions of $\overline{\mathcal{K}}$ we see immediately that

$$\mathfrak{A}(u) = \mathfrak{A}_0(u), \qquad \mathfrak{B}(u) = \mathfrak{B}_0(u).$$

It follows again that the operator K is the part of K_0 in $\overline{\mathcal{K}}$. We can then apply again the Weinstein method to approximate the eigenvalues of K. To do this we have to consider the subspace $\overline{\mathcal{K}_0} \ominus \overline{\mathcal{K}}$. It can be proved that this subspace is generated by a sequence $g^0_{II}(z, z_n)$ for any sequence $\{z_n\}$ dense in the domain $D_0 - D$, g^0_{II} being the function g_{II} corresponding to the domain D_0. If we take a finite number of functions $g^0_{II}(z, z_1), \ldots, g^0_{II}(z, z_n)$ and consider them as the functions p_k in the Weinstein method, we can form Weinstein's determinant $W(\zeta)$ and it is easily proved that this determinant is given by the formula

$$W(\zeta) = \left(\frac{-1}{\zeta}\right)^n \det. \left\{g^0_{II}\left(z_i, z_k, \frac{1}{\zeta}\right)\right\},$$

where $g^0_{II}(z, z', \xi)$ is the Green's function in the domain D_0 of $\Delta^2 u - \xi u = 0$, $u = \dfrac{\partial u}{\partial n} = 0$ on the boundary. When D_0 is a circle, this latter Green's function can be computed with the help of Bessel functions and we get in this way the possibility of computing lower bounds for the eigenvalues of clamped plates of any shape. The more the points $z_1, \ldots z_n$ are dense in $D_0 - D$, the better the lower bounds will be.

6. The applications of the ordinary Rayleigh-Ritz method are well known and very often used. This method will give upper bounds for a finite number of eigenvalues. To get upper bounds for all the eigenvalues we have to apply the generalized Rayleigh-Ritz method.

To show an example of application of the generalized Rayleigh-Ritz method consider two domains D and D_0 in the same way as in the last example of Weinstein's method, only now D_0 will be contained in D. We consider again the problem of vibrations of a clamped plate in both these domains. By a device used above, we will find that now the class $\overline{\mathcal{K}_0}$ is

a subclass of $\overline{\mathcal{K}}$ and if we take for D_0 a domain where the clamped plate problem is explicitly solvable, we will be in a position to apply the generalized Rayleigh-Ritz method.

As it may seem difficult in the present case to calculate the determinant $D(\zeta)$ and even to establish an explicit complete sequence $\{p_k\}$ in the subspace $\overline{\mathcal{K}} \ominus \overline{\mathcal{K}_0}$ we shall indicate briefly how this is to be done. We will take for D_0 a circle.

First, we take a complete sequence of functions $\{q_k(z)\}$ in the class $\overline{\mathcal{K}}$. This can be done in different ways. In the case when the boundary of D is given by an equation $\beta(z) \equiv \beta(x, y) = 0$ with β twice continuously differentiable in the closed domain $\bar{D}$ we can take for $\{q_k(z)\}$ the sequence of all functions $x^m y^n (\beta(z))^2$, $m, n = 0, 1, 2, \ldots$.

Then the projections p_k of q_k on the subspace $\mathcal{K}_1 = \overline{\mathcal{K}} \ominus \overline{\mathcal{K}_0}$ will form a complete sequence in $\mathcal{K}_1$. The function $p_k(z)$ is readily seen to be $= q_k(z)$ in $D - D_0$ and $= h_k(z)$ in D_0, where h_k is the harmonic function of order 2 ($\Delta\Delta h_k = 0$) in D_0 such that on the boundary C_0 of D_0 $h_k = q_k$ and $\dfrac{\partial h_k}{\partial n} = \dfrac{\partial q_k}{\partial n}$.

Now we have to calculate the function $p_k^{(0)} = P_0 K p_k$, where P_0 is the projection on $\overline{\mathcal{K}_0}$ and K is the operator given by (14) in the class $\overline{\mathcal{K}}$. In spite of the fact that K is not explicitly known (the function g_{II} for D is not known) we can calculate $p_k^{(0)}$ in the following way: $p_k^{(0)}$ is the solution of the equation

$$\Delta\Delta p_k^0 = p_k = h_k \text{ in } D_0, \qquad p_k^0 = \frac{\partial p_k^0}{\partial n} = 0 \text{ on } C_0.$$

We have then to calculate the functions $w_k(\zeta) \equiv w_k(z, \zeta) = R_\zeta^{(0)} p_k^{(0)}$. By the properties of the operator K_0, these functions appear as the solutions of the equation

$$w_k - \zeta \Delta\Delta w_k + h_k = 0 \text{ in } D_0, \qquad w_k = \frac{\partial w_k}{\partial n} = 0 \text{ on } C_0.$$

w_k as a function of ζ is a transcendental function which can always be written (by the use of spectral decomposition) as an infinite sum of simple fractions in ζ.

The general term of the determinant $D(\zeta)$ is $(Kw_k + Kp_k - \zeta p_k, p_l)$. By the definition of the scalar product in $\overline{\mathcal{K}}$ and the properties of the operator K, we obtain this term in the following form

$$\int_D (w_k + p_k) p_l \, d\omega - \zeta \int_D \Delta p_k \Delta p_l \, d\omega.$$

This shows already the possibility of calculating the determinant $D(\zeta)$ and of applying the generalized Rayleigh-Ritz method.

Before concluding the present paper, let us remark that the methods apply in a similar manner to differential operators in more than two variables.

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[2] Courant-Hilbert, *Methoden der Math. Physik*, vol. I, Chap. 6, and Vol. II, Chap. 7.

[3] This translation has already been used, especially by K. Friedrichs (e.g., in *Math. Ann.*, **109**, pp. 465 and 685, (1934) and in more recent papers), also by J. W. Calkin (*Trans. Am. Math. Soc.*, **45**, p. 369 (1939)).

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ON THE THEORY OF AGE-DEPENDENT STOCHASTIC BRANCHING PROCESSES

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We are interested in investigating the following mathematical problem which is of possible biological, chemical and physical interest. A particle existing at time $t_1 = 0$ is assumed to have a probability q_n, $n \geq 1$, of being transformed into n similar particles at some random time $t > 0$. Under the hypotheses that any particle has a life-length independent of its time of birth and the number of other particles existing at the time, and that there is no death, we require the probability distribution of $Z(t)$, the number of particles in existence at time t.

In our work, it is assumed that the random transformation times have a cumulative distribution $G(t)$, where $G(0) = 0$, and $G(\infty) = 1$. Depending upon the depth of the result we wish to prove, further assumptions are added. The most general of our results are derived under the assumption that $G(t)$ has a derivative $g(t)$, a density function, which is itself of bounded variation over any finite interval, and satisfies a slight additional restriction.

There has been a large amount of research done on the corresponding problem where the transformation time is independent of the age of the particle, cf., e.g., Harris,[3] Kolmogoroff,[4] Kolmogoroff and Sevastyanov,[5] Sevastyanov,[6] Yaglom.[7] To the best of the authors' knowledge, the problem in this paper has not been considered previously, although probabilities have been allowed to depend upon absolute time, cf. Arley,[1] where other references are given. Proofs of the results communicated here and further details will be published elsewhere at a later time.

A central rôle, as usual, is played by the generating function

$$F(s, t) = \sum_{r=1}^{\infty} P_r(t)s^r, \quad |s| \leq 1, \tag{1}$$

where

$$P_a(t) = \text{Prob}\,(Z(t) = r \text{ at time } t), r \geq 1. \tag{2}$$

Let as above q_n, $n \geq 1$, be the probability that when the particle is transformed, it is transformed into n particles, and let $h(s) = \sum_{n=1}^{\infty} q_n s^n$. Standard probabilistic arguments yield the non-linear integral equation

$$F(s, t) = \int_0^t h(F(s, t - y))dG(y) + s(1 - G(t)). \tag{3}$$

Non-linearity is a characteristic feature of the age-dependent theory as contrasted with the linearity of the Markoff processes of age-independent theory.

A routine application of the method of successive approximations yields

THEOREM 1. *Under the sole assumptions*

$$dG \geq 0, \qquad G(0) = 0, \qquad G(\infty) = 1, \tag{4}$$

equation (3) has for $|s| \leq 1$ a unique bounded solution possessing the elementary properties of a generating function, namely

$$F(s, t) = \sum_{r=1}^{\infty} P_r(t)s^r, \; P_r(t) \geq 0, \; |s| \leq 1, \tag{5a}$$

$$F(1, t) \equiv 1, \tag{5b}$$

$$F(s, 0) = s, \; P_1(t) = \left.\frac{\partial F}{\partial s}\right|_{s=0} = 1 - G(t). \tag{5c}$$

Furthermore, the moments

$$m_k(t) = \sum_{n=1}^{\infty} n^k P_n(t) \tag{6}$$

exist for $0 \leq t < \infty$, $k = 1, 2, \ldots$, provided that the moments $\sum_{n=1}^{\infty} n^k q_n$ exist for $k = 1, 2, \ldots$.

The explicit form of the $P_r(t)$ may now be determined by means of the above.

It is now of interest to investigate the distribution of the random variable

$$w(t) = Z(t)/E(Z(t)), \tag{7}$$

where $E(Z(t))$ is the expectation of Z, the first moment $m_1(t)$. The results

we obtain are generalizations of those of Harris,[3] and Yaglom,[7] derived under the assumption of age independence. We require first the asymptotic behavior of $E(Z(t))$. It is easy to show that the expectation satisfies the linear integral equation

$$u(t) = c_1 \int_0^t u(t - y)dG(y) + (1 - G(t)), \qquad (c_1 = h^1(1)), \quad (8)$$

which we recognize as the familiar linear equation of renewal theory.

The asymptotic behavior of the solutions of this equation has been extensively investigated by Feller.[2] From his results, we obtain

THEOREM 2. *Under the previous assumptions concerning $G(t)$, and the further assumptions that*

$$G(y) = \int_0^y g(u)du, \qquad \int_0^\infty e^{-bu}|dg| < \infty \qquad 9(a)$$

for some $b > 0$, whose value depends upon c_1, and

$$1 < c_1 = \sum_{n=1}^{\infty} nq_n < \infty, \qquad 9(b)$$

we obtain the asymptotic relations

$$m_k \sim a_k e^{kat}, \qquad k = 1, 2, \ldots, \qquad (10)$$

as $t \to \infty$, where a is defined as the positive root of

$$1 = c_1 \int_0^\infty e^{-ay} dG(y), \qquad (11)$$

provided that

$$\sum_{n=1}^{\infty} n^k q_n < \infty, \quad k = 1, 2, \ldots \qquad (12)$$

The result of (10) is also derived under other assumptions on $G(t)$ which permit it to have a step-function behavior. These results require more involved methods, and as they are of lesser importance, we shall not discuss them here.

Applying the results of Theorem 2, we derive the most important result of our researches

THEOREM 3. *Under the assumptions of Theorems 1 and 2, the random variable $w(t)$ converges in probability to a random variable w.*

Let $K(t)$ be the cumulative of $\bar{w}$, where $\bar{w} = Z(t)/e^{at}$, and set

$$\phi(s) = \int_0^\infty e^{sy} dK(y). \qquad (13)$$

It follows that

$$\phi(s) = \lim_{t \to \infty} F(s/e^{at}, t) \qquad (14)$$

and that

$$\phi(s) = \int_0^\infty h(\phi(s/e^{ay}))dG(y). \tag{15}$$

$K(t)$ is a continuous function of t. If we further assume that

$$\int_t^\infty g(y)dy \leq e^{-bt}, \quad t \geq t_1 \tag{16}$$

for some $b > 0$, then $K(t)$ is differentiable, so that $\phi(s)$ has the form

$$\phi(s) = \int_0^\infty e^{sy}k(y)dy. \tag{17}$$

From (16) we also derive bounds on the magnitude of $|\phi(it)|$ as $t \to \pm\infty$. These estimates are of value in computing $k(y)$ using the Fourier inversion formula.

These results are susceptible of generalization in several important directions. One may consider the case where death occurs, or the still more general case where death occurs and the probability of splitting is dependent on the time of birth. Then there are the problems of the distribution of ages, the number of splits in a given time interval, and so on. Finally, there is the case where there are particles of different types which give birth not only to those of the same type, but to those of other types. Biological mutation is included in this case. We hope to discuss these problems subsequently. Let us note that in many important situations a suitable transformation reduces the case with death to a case without death.

Finally, we may mention that several of the methods of the present paper are contained in essence in a paper by one of the authors, Harris.[2]

[1] Arley, N., *On the Theory of Stochastic Processes and Their Application to the Theory of Cosmic Radiation*, Copenhagen, 1943.

[2] Feller, W., "The Integral Equation of Renewal Theory," *Ann. Math. Statistics*, **12**, 243–268 (1943).

[3] Harris, T. E., "Branching Processes," *Ibid.*, to appear.

[4] Kolmogoroff, A., "Branching Stochastic Processes," *Compt. rend. (Doklady)*, **56**, 5–8 (1947) (Russian).

[5] Kolmogoroff, A., and Sevastyanov, B., "On the Asymptotic Form of the Probability for Stochastic Branching Processes," *Akad. Nauk (Doklady)*, **56**, 783–787 (1947) (Russian).

[6] Sevastyanov, B., "On the Theory of Stochastic Branching Processes," *Ibid.*, **59**, 1407–1409 (1948) (Russian).

[7] Yaglom, A., "Some Theorems in the Theory of Stochastic Branching Processes," *Ibid.*, **56**, 795–799 (1947) (Russian).

CONFORMAL MAPPING AND CONVERGENCE OF A POWER SERIES

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It is well known that there exist power series which map their circle of convergence onto a simply-connected domain D *and which converge at every point of the boundary of this circle.* For example, such is the case if the boundary of D is a Jordan curve; this follows from a theorem by Fejér.[1]

The present paper is devoted to the following question: do there exist power series with the above-mentioned convergence property, *which map their convergence circle onto the universal covering surface of a multiply-connected domain D?*

In answering this question we prove two lemmas (placed at the end of the paper) which, it is believed, have some interest for their own sake.

By way of introduction consider, for example, a power series $w = w(z) = \sum_{n=0}^{\infty} a_n z^n$ mapping the unit circle C, $|z| < 1$, onto the universal covering surface S of the circular ring $1/2 < |w| < 1$. Consider on S all the straight lines which join the points $1/2$ and 1. Their images on C form a doubly infinite sequence of analytic curves (c_n), $n = \ldots, -1, 0, +1, \ldots$, having the following properties: 1° each curve c_n is situated in the interior of C and joins two different boundary points, 2° two different curves of (c_n) never have a point in common, 3° every continuous curve situated in C and joining a point of c_{n-1} with a point of c_{n+1} must intersect c_n, and 4° the curves (c_n) tend to the boundary of C as $n \to \infty$ and as $n \to -\infty$. The three first properties are evident, the fourth is seen in the following way.

Let z_n be the point (or one of the points) of c_n which has the largest distance from the boundary of C. The sequence (z_n) has at least one accumulation point z', and z' must be located on the boundary of C, for, otherwise, its image would be an interior point of S, and this is impossible. Hence $\lim_{n \to \pm\infty} |z_n| = 1$ by the above property 3°.

Now consider in C the radius vector from the origin to the point $z' = e^{i\varphi}$. This radius intersects an infinite number of curves c_n, and so we can choose a sequence of points $r_k e^{i\varphi}$, $k = 1, 2, \ldots$, lying on it such that 1° $r_k < r_{k+1}$, $k = 1, 2, \ldots$, 2° $\lim_{k \to \infty} r_k = 1$, and 3° $w(r_{2k-1}e^{i\varphi}) > 1/2$ and $w(r_{2k}e^{i\varphi}) < -1/2$, $k = 1, 2, \ldots$. Therefore, $\lim_{r \to 1-0} w(re^{i\varphi})$ cannot exist, and, by Abel's theorem, $\sum a_n e^{in\varphi}$ cannot converge.

Now, consider the more general case in which $\sum a_n z^n$ maps C onto the

universal covering surface of an arbitrary multiply-connected bounded domain D. The boundary of D then consists of an exterior contour B and a remainder B' consisting of one or more interior contours or points. By an argument analogous to the one above, we see that, if B' consists of more than one point, then $\sum a_n z^n$ must diverge at two boundary points at least.

Our only chance then to construct a power series satisfying the desired convergence property is to choose as D a bounded domain, whose boundary consists of an exterior contour and one isolated point.

The Taylor series $\sum_{n=0}^{\infty} c_n z^n$ of the function[2] $w = \exp \frac{z+1}{z-1}$, where we have written exp a for e^a, has the above-mentioned mapping property. In fact, it is easily verified: 1° that this series has the convergence radius one, 2° that the function $u = \frac{z+1}{z-1}$ maps the unit circle of the z-plane onto the half-plane $Ru < 0$ of the u-plane and the point $z = 1$ into the point $u = \infty$, and 3° that the function $w = e^u$ maps the half-plane $Ru < 0$ onto the universal covering surface of the circle $|w| < 1$ punctured at $w = 0$. Here, the point $u = \infty$ corresponds in a certain sense to the point $w = 0$. The function $w = \exp \frac{z+1}{z-1}$ has of course an essential singularity at $z = 1$ with the Picard exceptional values 0 and ∞.

The coefficient c_n of the power series

$$w = \exp \frac{z+1}{z-1} = \sum_{n=0}^{\infty} c_n z^n, \qquad |z| < 1, \tag{1}$$

can be written in the form

$$c_n = \frac{1}{2\pi i} \int_{C_\epsilon} \exp \frac{z+1}{z-1} \frac{dz}{z^{n+1}} \tag{2}$$

where C_ϵ is the boundary of the common part of the domains $|z| < 1$ and $|z - 1| > \epsilon$, $0 < \epsilon < 1$. Now the function $\exp \frac{z+1}{z-1}$ is bounded for $|z| \leq 1$ and $z \neq 1$, and hence we can let $\epsilon \to 0$ in (2), giving

$$c_n = \frac{1}{2\pi i} \int_{|z|=1} \exp \frac{z+1}{z-1} \frac{dz}{z^{n+1}}.$$

Making the variable transformation $z = e^{i\theta}$ and observing that c_n is real, we get

$$c_n = \frac{1}{2\pi}\int_{-\pi}^{\pi} \exp \frac{e^{i\theta}+1}{e^{i\theta}-1}\frac{d\theta}{e^{in\theta}} = \frac{1}{2\pi}\int_{-\pi}^{\pi}\left\{\cos\left(\cot\frac{\theta}{2}\right)\right.$$

$$\left. - i\sin\left(\cot\frac{\theta}{2}\right)\right\}\left\{\cos n\theta - i\sin n\theta\right\}d\theta = \frac{1}{2\pi}\int_{-\pi}^{\pi}\cos\left(\cot\frac{\theta}{2}\right)$$

$$\cos n\theta\, d\theta - \frac{1}{2\pi}\int_{-\pi}^{\pi}\sin\left(\cot\frac{\theta}{2}\right)\sin n\theta\, d\theta = a_n - b_n,$$

let us say.

We write

$$a_n = \frac{1}{\pi}\int_0^{\pi}\cos\frac{2}{\theta}\cos n\theta\, d\theta + \frac{1}{\pi}\int_0^{\pi}\left\{\cos\left(\cot\frac{\theta}{2}\right) - \cos\frac{2}{\theta}\right\}\cos n\theta\, d\theta =$$

$$a_n' + a_n''.$$

Here the series $\sum a_n'$ converges by Lemma 1. The coefficient a_n'' is the nth cosine coefficient of the Fourier series of the even periodic function $g(\theta)$, which coincides in $(0, \pi)$ with the function

$$\frac{1}{2}\left\{\cos\left(\cot\frac{\theta}{2}\right) - \cos\frac{2}{\theta}\right\} = \frac{1}{2}\left\{\cos\left(\frac{2}{\theta} + 0(\theta)\right) - \cos\frac{2}{\theta}\right\} =$$

$$-\sin\left(\frac{2}{\theta} + 0(\theta)\right)\sin 0(\theta). \quad (3)$$

Now the above-mentioned Fourier series converges to zero for $\theta = 0$ by Dini's test, for the function $g(\theta)/\theta$ is integrable in $(0, \pi)$, as is easily seen by the last expression (3). Hence the series $\sum a_n''$ is convergent.

Analogously we write

$$b_n = \frac{1}{\pi}\int_0^{\pi}\sin\frac{2}{\theta}\sin n\theta\, d\theta + \frac{1}{\pi}\int_0^{\pi}\left\{\sin\left(\cot\frac{\theta}{2}\right) - \sin\frac{2}{\theta}\right\}\sin n\theta\, d\theta =$$

$$b_n' + b_n''$$

and observe that the series $\sum b_n'$ converges by Lemma 2. Here b_n'' is the nth cosine coefficient of the conjugate series of the Fourier series of the odd periodic function $h(\theta)$, which coincides in $(0, \pi)$ with

$$\frac{1}{2}\left\{\sin\left(\cot\frac{\theta}{2}\right) - \sin\frac{2}{\theta}\right\} = \frac{1}{2}\left\{\sin\left(\frac{2}{\theta} + 0(\theta)\right) - \sin\frac{2}{\theta}\right\} =$$

$$\cos\left(\frac{2}{\theta} + 0(\theta)\right)\sin 0(\theta).$$

Hence the conjugate series converges for $\theta = 0$ by Dini's test, since the function $h(\theta)/\theta$ is integrable in $(0, \pi)$. Therefore the series $\sum b_n''$ is convergent.

Summing up our results we find that the series (1) converges for $z = 1$. And its sum is zero by Abel's theorem, since, writing $z = re^{i\theta}$, we have $\lim_{r\to 1-0} w = 0$, where w is defined by (1). Further it is evident that the series (1) converges for every fixed z with $|z| = 1$ and $z \neq 1$ to a value with modulus one.

Thus we can state our main result in the following way:

The power series (1) maps the interior of the unit circle onto the universal covering surface of the domain $0 < |w| < 1$ of the w-plane and it converges at every point of the boundary of its convergence circle, though not uniformly.

LEMMA 1. *Consider the Fourier series of the even periodic function $g(\theta)$ which in $(0, \pi)$ coincides with $\cos \frac{2}{\theta}$:*

$$g(\theta) \sim \frac{1}{2} a_0 + \sum_{n=1}^{\infty} a_n \cos n\theta.$$

This series converges to zero for $\theta = 0$.

Proof: It is sufficient[3] to show that

$$\int_0^1 \frac{g(\theta) \sin n\theta}{\theta} d\theta \to 0 \text{ as } n \to \infty. \tag{4}$$

We write

$$\int_0^1 \cos \frac{2}{\theta} \frac{\sin n\theta}{\theta} d\theta = \frac{1}{2} \int_0^1 \sin \left(n\theta - \frac{2}{\theta}\right) \frac{d\theta}{\theta} + \frac{1}{2} \int_0^{\sqrt{2/n}} \sin \left(n\theta + \frac{2}{\theta}\right) \frac{d\theta}{\theta} + \frac{1}{2} \int_{\sqrt{2/n}}^1 \sin \left(n\theta + \frac{2}{\theta}\right) \frac{d\theta}{\theta} = \frac{1}{2} (P + Q + R). \tag{5}$$

In the integral P we make the substitution $n\theta - 2/\theta = t$, $\theta = (t + \sqrt{t^2 + 8n})/2n$ and we find

$$P = \int_{-\infty}^{n-2} \frac{\sin t}{\sqrt{t^2 + 8n}} dt = \int_{-\infty}^{0} + \int_0^{n-2}.$$

The second mean-value theorem now gives

$$P = \frac{1}{\sqrt{8n}} \int^{0} \sin t \, dt + \frac{1}{\sqrt{8n}} \int_0^{\tau'} \sin t \, dt,$$

where $-\infty < \tau < 0$ and $0 < \tau' < n - 2$, and so

$$|P| \leq \frac{1}{\sqrt{2n}}. \tag{6}$$

To estimate Q we use the substitution $n\theta + 2/\theta = t$, $\theta = (t - \sqrt{t^2 - 8n})/2n$, and we obtain

$$Q = \int_{\sqrt{8n}}^{\infty} \frac{\sin t}{\sqrt{t^2 - 8n}}\, dt.$$

Choose the integer p such that $(p-1)\pi < \sqrt{8n} < p\pi$. Then

$$Q = \left[\int_{\sqrt{8n}}^{p\pi} + \sum_{k=1}^{\infty} \int_{(p+k-1)\pi}^{(p+k)\pi}\right] \frac{\sin t}{\sqrt{t^2 - 8n}}\, dt = u + \sum_{k=1}^{\infty} \sum u_k,$$

say. Here $\sum u_k$ is an alternating series whose terms decrease monotonically in absolute value, and so the modulus of its sum is less than $|u_1|$. Hence

$$|Q| < |u| + |u_1| < \int_{\sqrt{8n}}^{(p+1)\pi} \frac{|\sin t|}{\sqrt{t^2 - 8n}}\, dt < \int_{\sqrt{8n}}^{\sqrt{8n}+2\pi} \frac{dt}{\sqrt{t^2 - 8n}} < \frac{1}{2\sqrt[4]{2n}} \int_{\sqrt{8n}}^{\sqrt{8n}+2\pi} \frac{dt}{\sqrt{t - \sqrt{8n}}}$$

or

$$|Q| < \frac{\sqrt{2\pi}}{\sqrt[4]{2n}}. \tag{7}$$

Finally, to get an upper bound for $|R|$, we set $n\theta + 2/\theta = t$, $\theta = (t + \sqrt{t^2 - 8n})/2n$ and obtain

$$R = \int_{\sqrt{8n}}^{n+2} \frac{\sin t}{\sqrt{t^2 - 8n}}\, dt.$$

But this expression can be estimated in just the same way as Q; the only difference is that the series Σu_k now has only a finite number of terms. Hence we also have

$$|R| < \frac{\sqrt{2\pi}}{\sqrt[4]{2n}} \tag{8}$$

Summing up the results (6), (7) and (8) we see that the desired relation (4) holds, and Lemma 1 is proved.[4]

LEMMA 2. *Consider the Fourier series of the odd periodic function $h(\theta)$ which in $(0, \pi)$ coincides with $\sin \frac{2}{\theta}$:*

$$h(\theta) \sim \sum_{n=1}^{\infty} b_n \sin n\theta. \tag{9}$$

Then the series $\sum_{n=1}^{\infty} b_n$ *is convergent.*

Proof: Here b_n is the nth cosine coefficient of the conjugate series of the series (9), and we have to show that this conjugate series converges for $\theta = 0$. To this end it is sufficient[5] to prove the three relations:

$$\int_0^t h(\theta)\, d\theta = o(t) \text{ as } t \to +0, \tag{10}$$

$$\lim_{\epsilon \to +0} \int_\epsilon^1 h(\theta) \frac{d\theta}{\theta} \text{ exists,} \tag{11}$$

and

$$\int_{1/n}^1 h(\theta) \frac{\cos n\theta}{\theta}\, d\theta \to 0 \text{ as } n \to \infty. \tag{12}$$

Formula (10) is immediate:

$$\int_0^t \sin\frac{2}{\theta}\, d\theta = \int_0^t \left\{\sin\frac{2}{\theta} + \theta\cos\frac{2}{\theta}\right\} d\theta + o(t) = \frac{t^2}{2}\cos\frac{2}{t} + o(t).$$

The statement (11) is easily verified by the substitution $1/\theta = t$. Finally to demonstrate (12), we write

$$\int_{1/n}^1 \sin\frac{2}{\theta}\frac{\cos n\theta}{\theta}\, d\theta = -\frac{1}{2}\int_{1/n}^1 \sin\left(n\theta - \frac{2}{\theta}\right)\frac{d\theta}{\theta} + \frac{1}{2}\int_{1/n}^{\sqrt{2/n}} \sin\left(n\theta + \frac{2}{\theta}\right)\frac{d\theta}{\theta} + \frac{1}{2}\int_{\sqrt{2/n}}^1 \sin\left(n\theta + \frac{2}{\theta}\right)\frac{d\theta}{\theta}.$$

These terms can be treated in the same way as the corresponding terms of (5), giving (12), and Lemma 2 is proved.

[1] *Compt. rend., Paris*, **156**, p. 46 (1913). Montel, *Leçons sur les familles normales*, Paris, 1927, p. 119. Further examples are given in the author's article, "Sur la convergence des séries potentielles," *Arkiv Mat., Astron., Fysik, Uppsala*, **31B**, no. 6 (1944).

[2] After submitting this paper I have learned that Pringsheim (*Sitzber. bayer. Akad., Math. u. Phys. Klasse*, p. 92 (1900)) has studied the convergence properties of the Taylor series of $\exp\frac{z}{z-1}$, though from a point of view different from the one adopted here.

[3] See Hardy-Rogosinski, *Fourier Series*, Cambridge, 1944, p. 38, Theorem 50.

[4] In proving Lemma 1 we have used Cauchy integrals instead of Lebesgue integrals in some instances. This can easily be avoided in the following way: use ϵ, $0 < \epsilon < \sqrt{2/n}$, as lower bound in the integral (4), and repeat the whole argument giving

$$\left|\int_\epsilon^1 \cos\frac{2}{\theta}\frac{\sin n\theta}{\theta}\, d\theta\right| < \frac{1}{\sqrt{2n}} + 2\frac{\sqrt{2\pi}}{\sqrt[4]{2n}}; \text{ now let } \epsilon \to 0.$$

[5] See Hardy-Rogosinski, *loc. cit.*, p. 48, Theorem 61.

ESSENTIAL MULTIPLICITY AND LEBESGUE AREA

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1. Introduction.—This note exhibits some applications of standard methods of algebraic topology to the theory of area.

We suppose that M is a k-dimensional orientable manifold, X is a compact locally connected subset of M, Y is k-dimensional Euclidean space and C is the set of all continuous functions on X to Y, which is metrized by the function d such that

$$d(f, g) = \sup_{x \in X} |f(x) - g(x)| \qquad \text{for } f, g \in C.$$

For $f \in C$ and each open subset U of Y we define $F(f, U)$ to be the family of all components of the set

$$X \cap_x E[f(x) \in U].$$

We observe that if f, U are as above and $y \in U$, then there are at most finitely many $A \in F(f, U)$ for which $A \cap_x E[f(x) = y]$ is non-vacuous.

Let $H^n(A, B)$ be the n-dimensional Cech cohomology group of A modulo B with integer coefficients, whenever $A \supset B$ are compact.

We recall that if $A \supset B$ are compact subsets of a k-dimensional manifold for which $A - B$ is non-vacuous and connected, then $H^k(A, B)$ is infinite cyclic or trivial according as B does or does not contain the boundary of A.

Let L_k be the k-dimensional Lebesgue measure over Y.

2. Definition of the Multiplicity.—If $f \in C$, U is an open connected subset of Y with compact closure and $A \in F(f, U)$, then $D(f, U, A)$ is the non-negative integer defined as follows: In case $H^k(\text{Clos } A, \text{Bdry } A)$ is infinite cyclic, the homomorphism of $H^k(\text{Clos } U, \text{Bdry } U)$ into $H^k(\text{Clos } A, \text{Bdry } A)$ induced by $(f | \text{Clos } A)$ relates to a generator of the first group an integral multiple of a generator of the second group, and $D(f, U, A)$ is defined as the absolute value of the multiplier, which is independent of the choice of generators.[1] In case $H^k(\text{Clos } A, \text{Bdry } A)$ is trivial, we define $D(f, U, A) = 0$.

If f and U are as above, then the set of all those $A \in F(f, U)$ for which the f image of A contains U is finite. Hence $D(f, U, A) = 0$ for all but finitely many $A \in F(f, U)$, and we define the non-negative integer

$$D(f, U) = \sum_{A \in F(f, U)} D(f, U, A).$$

It is readily seen that if $f \in C$ and $U_1 \supset U_2$ are open connected subsets of Y with compact closure, then $D(f, U_1) \leqslant D(f, U_2)$.

For each $y \in Y$ we define $M(f, y)$, *the essential multiplicity with which f assumes the value y*, as the supremum of $D(f, U)$ for all open connected neighborhoods U of y with compact closure. Since $D(f, U)$ is monotone with respect to U on the set of all these neighborhoods partially ordered by inclusion, $\supset$, we have

$$M(f, y) = \lim_{n \to \infty} D(f, U_n)$$

whenever $U_1 \supset U_2 \supset U_3 \supset \ldots$ are any such neighborhoods whose intersection contains only y.

It is easy to check that if $f, g \in C$ and $U_1 \supset U_2$ are open connected subsets of Y with compact closures such that

$$d(f, g) \leqslant \text{distance } (U_2, Y - U_1),$$

then

$$D(g, U_2) \geqslant D(f, U_1).$$

It follows that the function M is lower semicontinuous on the cartesian product space $(C \times Y)$.

3. Approximation Theorems.—The Hopf extension theorem yields the following information:

If $f \in C$, U is an open convex cell with compact closure contained in Y, $A \in F(f, U)$ and $D(f, U, A) = 0$, then there is a $g \in C$ such that

$$\begin{aligned} g(x) &= f(x) && \text{for } x \in X - A, \\ g(x) &\in \text{Bdry } U && \text{for } x \in A. \end{aligned}$$

If f, U, A are as above, but $D(f, U, A) > 0$, and if $y \in U$, then there is a $g \in C$ and an open cell B such that Clos $B \subset A$,

$$\begin{aligned} g(x) &= f(x) && \text{for } x \in X - A, \\ g(x) &\in \text{Bdry } U && \text{for } x \in A - B, \\ g(x) &\in U && \text{for } x \in B, \\ &(g \mid \text{Clos } B) \text{ is simplicial,} \\ &A \cap_x E[g(x) = y] \text{ has one element,} \\ &A \cap_x E[g(x) = z] \text{ has } D(f, U, A) \text{ elements} \end{aligned}$$

for L_k almost all z in U.

Furthermore the cell B may be prescribed.

Applying the preceding two lemmas to all those $A \in F(f, U)$ for which $A \cap_x E[f(x) = y]$ is non-vacuous, and a modification by central projection

from y onto Bdry U to all other $A \in F(f, U)$, we prove:

If $f \in C$, U is an open convex cell with compact closure contained in Y, $y \in U$, and n is the number of those $A \in F(f, U)$ for which $D(f, U, A) \neq 0$, then there exist a map $g \in C$ and open cells $B_1, \ldots, B_n$, whose closures are contained in distinct elements of $F(f, U)$, such that

$g(x) = f(x)$ *whenever* $f(x) \in Y - U$,

$g(x) \in$ Bdry U *whenever* $f(x) \in U$ *and not* $x \in \overset{n}{\underset{j=1}{\cup}} B_j$,

$g(x) \in U$ *whenever* $x \in \overset{n}{\underset{j=1}{\cup}} B_j$,

$\left(g \mid \overset{n}{\underset{j=1}{\cup}} \text{Clos } B_j\right)$ *is simplicial,*

$E^{x}[g(x) = y]$ *has n elements,*

$E^{x}[g(x) = z]$ *has $D(f, U)$ elements for L_k almost all z in U.*

This theorem concerning the modification of a mapping on the counterimage of a single cell, may be applied at once to modify a map on the counterimage of the union of any finite set of disjoint cells. This yields the following proposition:

If $f \in C$ and $U_1, \ldots, U_m$ are those k-cells of a polyhedral subdivision of Y which meet range f, then there exist a map $g \in C$ and open cells $B_1, \ldots, B_n$, whose closures are contained in distinct elements of $\overset{m}{\underset{i=1}{\cup}} F(f, U_i)$, such that

$g(x) = f(x)$ *whenever* $f(x) \in Y - \overset{m}{\underset{i=1}{\cup}} U_i$,

$g(x) \in$ Bdry U_i *whenever* $f(x) \in U_i$ *and not* $x \in \overset{n}{\underset{j=1}{\cup}} B_j$,

$g(x) \in U_i$ *whenever* $f(x) \in U_i$ *and* $x \in B_j$,

$\left(g \mid \overset{n}{\underset{j=1}{\cup}} B_j\right)$ *is simplicial,*

$E^{x}[g(x) = z]$ *has $D(f, U_i)$ elements for L_k almost all z in U_i,*

g maps $X - \overset{n}{\underset{j=1}{\cup}} B_j$ into the $k-1$ skeleton of the polyhedral subdivision of Y.

If, in addition, X is a polyhedron, then $B_1, \ldots, B_n$ may be chosen as cells of a refinement of any given polyhedral subdivision of X, and for each positive number ϵ there is a simplicial map $h \in C$ such that $d(g, h) < \epsilon$,

$$g(x) = h(x) \quad \text{for } x \in \overset{n}{\underset{j=1}{\cup}} B_j,$$

h maps $X - \overset{n}{\underset{j=1}{\cup}} B_j$ into the $k-1$ skeleton of the subdivision of Y.

If diameter $U_i < \epsilon$ for $i = 1, \ldots, m$, then $d(f, h) < \epsilon$.

4. *Application to Area.*—Let G be the function on C such that

$$G(f) = \int_Y M(f, y) dL_k y \quad \text{for } f \in C.$$

The lower semicontinuity of M and Fatou's lemma imply that the Geöcze area G is lower semicontinuous on C.

If $f \in C$ and P is a finite family of disjoint open connected subsets of Y with compact closures, then

$$\sum_{U \in P} D(f, U) \cdot L_k(U) \leqslant G(f),$$

because $D(f, U) \leqslant M(f, y)$ for $y \in U \in P$.

The fact that $G(f)$ is actually the supremum of such sums is a consequence of the following proposition:

If $f \in C$ and $P_1, P_2, P_3, \ldots$ are such finite families of disjoint open connected subsets of Y with compact closures that

$$\lim_{n \to \infty} \sup_{U \in P_n} \text{diameter } U = 0,$$
$$\lim_{n \to \infty} L_k (\text{range } f - \bigcup_{U \in P_n} U) = 0,$$

then

$$\lim_{n \to \infty} \sum_{U \in P_n} D(f, U) \cdot L_k(U) = G(f).$$

To prove this by contradiction we may assume, after passage to a subsequence if necessary, that

$$\lim_{n \to \infty} \sum_{U \in P_n} D(f, U) \cdot L_k(U) < G(f),$$

$$\sum_{n=1}^{\infty} L_k (\text{range } f - \bigcup_{U \in P_n} U) < \infty,$$

whence

$$L_k[\bigcap_{m=1}^{\infty} \bigcup_{n=m}^{\infty} (\text{range } f - \bigcup_{U \in P_n} U)] = 0.$$

We define

$$r(U, y) = 1 \text{ for } y \in U, \; r(U, y) = 0 \text{ for } y \in Y - U,$$

and observe that

$$\lim_{n \to \infty} \sum_{U \in P_n} D(f, U) \cdot r(U, y) = M(f, y)$$

for $y \in \text{range } f - \bigcap_{m=1}^{\infty} \bigcup_{n=m}^{\infty} (\text{range } f - \bigcup_{U \in P_n} U)$, hence for L_k almost all y in range f.

Now Fatou's lemma implies

$$\lim_{n \to \infty} \sum_{U \in P_n} D(f, U) \cdot L_k(U) = \lim_{n \to \infty} \int_{\text{range } f} \sum_{U \in P_n} D(f, U) \cdot r(U, y) \, dL_k y \geqslant G(f).$$

This contradiction completes the proof.

If X is a polyhedron, $f \in C$ and $\epsilon > 0$, we may choose P as the set of all those k-cells of a polyhedral subdivision of Y which meet range f and so that diameter $U < \epsilon$ for $U \in P$. Then the last theorem of Section 3 yields a simplicial map $h \in C$ for which $d(f, h) < \epsilon$ and

$$G(h) = \sum_{U \in P} D(f, U) \cdot L_k(U) \leqslant G(f).$$

We conclude that *if X is a polyhedron, then G is the Lebesgue area.*

For the special case in which $k = 2$ and X is a 2-cell this result is substantially due to Lamberto Cesari, who has also very ingeniously solved the corresponding much deeper problem for maps of a 2-cell into 3-space.[2] The extension to maps of k-cells into n-space, with $2 \leqslant k < n$ and $n > 3$, appears still remote.

5. *Essential Components and Stable Multiplicity.*—If $f \in C$, $y \in Y$ and T is a component of $E[f(x) = y]$, then T is said to be *essential* if and only if $D(f, U, A) > 0$ whenever U is an open connected neighborhood of y with compact closure and $T \subset A \in F(f, U)$.

Let $E(f, U)$ be the number of those $A \in F(f, U)$ for which $D(f, U, A) > 0$, and let $S(f, y)$ be the supremum of $E(f, U)$ with $y \in U$. Clearly $S(f, y) \leqslant M(f, y)$.

We observe that if $U_1 \supset U_2$ and $D(f, U_1) < D(f, U_2)$, then $E(f, U_1) < E(f, U_2)$. Hence $M(f, y) = \infty$ if and only if $S(f, y) = \infty$.

The essential components are all sets of the type

$$\bigcap_{n=1}^{\infty} A_n, \text{ where } A_1 \supset A_2 \supset A_3 \supset \ldots, D(f, U_n, A_n) > 0,$$

$U_1 \supset U_2 \supset U_3 \supset \ldots$ and $\bigcap_{n=1}^{\infty} U_n = \{y\}$. Hence $S(f, y)$ *is the number of essential components of* $E[f(x) = y]$.

The function S is lower semicontinuous on $(C \times Y)$.

Let $N(f, y)$ be the number (possibly ∞) of x for which $f(x) = y$. Clearly $S(f, y) \leqslant N(f, y)$. Our first approximation theorem implies

$$S(f, y) = \liminf_{g \to f} N(g, y),$$

so that $S(f, y)$ *is the stable multiplicity with which f assumes y.*

For the special case in which $k = 2$ and X is a closed 2-cell these results are substantially due to Rado and Reichelderfer.[3] The function S has also been used by the author.[4]

Cesari has shown,[5] by a method depending significantly on the existence of covering maps of the punctured plane with prescribed degree, that if

$k = 2$, X is a 2-cell and $f \in C$, then the set of all those y for which $S(f, y) < M(f, y)$ is countable. However, if $k > 2$, this inequality may hold on a set of positive measure; for instance f may wrap a solid cube several times around an arc of positive volume. Hence the results of the preceding section indicate that M is more suitable than S for the theory of area.

[1] Here Bdry A refers to the relative topology of X.

[2] Cesari, L., "Una ugualianza fondamentale per l'area delle superficie," *Atti della Reale Accademia d'Italia, Memorie*, **14**, 891–951 (1944).

[3] Rado, T., and Reichelderfer, P. V., "A Theory of Absolutely Continuous Transformations in the Plane," *Trans. Am. Math. Soc.*, **49**, 258–307 (1941).

[4] Federer, H., "Coincidence Functions and Their Integrals," *Ibid.*, **59**, 441–466 (1946).

[5] Cesari, L., "Sui punti di diramazione delle trasformazioni continue e sull' area delle superficie in forma parametrica," *Univ. Roma e Ist. Naz. Alta Mat. Rend. Mat. e Appl.*, ser. 5, **3**, 37–62 (1942).

SOME NEW RESULTS ON PARTITIONS

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This paper contains the statements of five theorems on partitions, the proofs of which will appear in a series of papers in another American journal, devoted entirely to mathematics.

Euler's identity

$$\frac{1}{(1-x)(1-x^3)(1-x^5)\cdots} = (1+x)(1+x^2)(1+x^3)\cdots \quad (1)$$

may be paraphrased as follows:

The number of partitions of n into odd parts is equal to the number of partitions of n into distinct parts.

Definition 1: The *rank* of a partition is the excess of the maximum part over the number of parts.[1]

Definition 2: $D_r(n)$ = the number of partitions of n into distinct parts, the rank of each partition being r.

Definition 3: $U_{2r+1}(n)$ = the number of partitions of n into odd parts, the maximum part being $2r + 1$.

It is clear that the rank of a partition into distinct parts cannot be negative. Hence Euler's theorem may be written

$$U_1(n) + U_3(n) + U_5(n) + \cdots = D_0(n) + D_1(n) + D_2(n) + \cdots \quad (2)$$

Our first theorem sets up a more refined correspondence between the terms in the right and left members of (2).

THEOREM 1. *For all* $n \geq 1$, $r \geq 0$, *we have*

$$U_{2r+1}(n) = D_{2r+1}(n) + D_{2r}(n). \tag{3}$$

Our second theorem is a paraphrase of the double identity

$$\begin{aligned} &1 - \frac{x}{1+x} + \frac{x^3}{(1+x)(1+x^3)} - \frac{x^5}{(1+x)(1+x^3)(1+x^5)} + \cdots \\ &= 1 - x + (1+x)x^2 - (1+x)(1+x^2)x^3 + (1+x)(1+x^2)(1+x^3)x^4 - \cdots \\ &= 1 - x + x^2 - x^5 + x^7 - x^{12} + x^{15} - x^{22} + \cdots, \end{aligned} \tag{4}$$

the exponents in the last series being the pentagonal numbers $\frac{1}{2}(3k^2 \pm k)$.

Definition 4: $Q_a(n)$ = the number of partitions of n into distinct parts, the maximum part being $\equiv a \pmod 2$, $a = 0, 1$.

Definition 5: $Q_b^*(n)$ = the number of partitions of n into odd parts, the maximum part being $\equiv b \pmod 4$, $b = 1, 3$.

THEOREM 2.

(i) $Q_1^*(2n) = Q_0(2n)$; $\quad Q_3^*(2n) = Q_1(2n)$.

(ii) $Q_1^*(2n+1) = Q_1(2n+1)$; $\quad Q_3^*(2n+1) = Q_0(2n+1)$.

(iii) $Q_0(n) - Q_1(n) = +1$ if $n = \frac{1}{2}(3k^2 + k)$, $k \geq 0$,
$= -1$ if $n = \frac{1}{2}(3k^2 - k)$, $k > 0$,
$= 0$ otherwise.

Part (iii) of Theorem (2) bears some resemblance to the famous pentagonal number theorem of Euler, but we have not been able to establish any real connection between the two theorems.

Definition 6: $p(n)$ = the number of unrestricted partitions of n; $p(0) = 1$; $p(n) = 0$ for $n < 0$.

Definition 7: $P_r(n)$ = the number of partitions of n with rank r; $P_0(0) = 1$; $P_r(n) = 0$ for $r \neq 0$, $n \leq 0$.

THEOREM 3. *For* $k > 1$, $r > max\ (0, k-5)$,

$$P_r(r+k) = p(k-1) - p(k-2). \tag{5}$$

THEOREM 4.

(i) $P_0(n+1) + P_0(n) + 2P_2(n-1) = p(n+1) - p(n)$ $\quad (n > 0)$.

(ii) $P_0(n-1) - P_1(n) + P_2(n-2) - P_4(n-3) = 0$ $\quad (n > 1)$.

(iii) $P_0(n) - P_1(n-1) - P_2(n-1) + P_3(n-2) = 0$ $\quad (n > 1)$.

(iv) $P_{r+1}(n) - P_r(n-1) - P_{r+2}(n-r-2) + P_{r+4}(n-r-3) = 0$
$\quad (r > 0, n > 0)$.

We observe that (i) enables us to determine the unrestricted partition

function from the two functions $P_0(n)$ and $P_3(n)$. In fact, if we sum (i) for $1 \leqslant n \leqslant N$, we obtain

$$p(N+1) = P_0(N+1) + 2P_0(N) + 2\sum_{n=1}^{N-1}(P_0(n) + P_3(n)). \quad (6)$$

Equations (ii), (iii), (iv), together with the obvious remark that $P_r(n) = P_{-r}(n)$, yield the result that the functions $P_r(n)$ can all be determined from the functions $P_0(n)$, $P_1(n)$, $P_2(n)$.

Definition 8: $L(n)$ = the number of partitions of n into distinct parts, the minimum part being odd.

THEOREM 5. *For $n \geqslant 1$, $L(n)$ is odd if and only if n is a square.* It is possible to obtain more precise information about the arithmetic properties of $L(n)$ for special forms of n. We shall restrict ourselves to the remark that

$$L(p^{2ns}) \equiv 1 \pmod 4$$

if p is a prime.

[1] To the best of our knowledge, this concept was first introduced by F. J. Dyson in the *American Mathematical Monthly*, August-September, 1947, p. 418.

INDEX

Abelian groups (Mackey), 156.
Age dependent stochastic processes (Bellman and Harris), 601.
Aging and growth cessation (Lansing), 304.
AJL, S. J., and WERKMAN, C. H. Enzymatic Fixation of Carbon Dioxide in α-Keto glutaric Acid, 491.
α-Ketoglutaric acid (Ajl and Werkman), 491.
Amino acid in *Drosophila* (Blumel and Kirby), 561.
Amino acids and growth (Sanders and Burkholder), 516
ANCHEL, M., HERVEY, A., KAVANAGH, F., POLATNICK, J., and ROBBINS, W. J. Antibiotic Substances from Basidiomycetes, III. *Coprinus Similis* and *Lentinus Degener*, 498.
ANDERSON, E. G. On the Frequency and Transmitted Chromosome Alterations and Gene Mutations Induced by Atomic Bomb Radiations in Maize, 387.
Antibiotics (Garson and Waksman), 232.
Antibiotics from Basidiomycetes (Anchel, Hervey, Kavanagh, Polatnick and Robbins), 498.
Antigenic differences in *Paramecium* (Sonneborn), 413; (Beale), 418.
Appell polynomials (Boas), 481.
Arginine metabolism (Houlahan and Mitchell), 465.
Arithmetic functions (Bellman), 149.
ARONSZAJN, N. Rayleigh-Ritz and A. Weinstein Methods for Approximation of Eigenvalues. I. Operators in a Hilbert Space, 474.
——. II. Differential Operators, 594.
Ascent of Koroyanitu (Smith), 579.
AsH_3, AsD_3, PH_3 spectra (McConaghie and Nielsen), 455.
Atomic bomb radiations and maize (Anderson), 387.
Average value of arithmetic functions (Bellman), 149.

Bacteria, nutritional mutants of (Ryan), 425; predictable (Witkus), 442.
Bacterial virus (Hershey and Rotman), 89; (Price), 317.
BARGMANN, V., and WIGNER, E. P. Group Theoretical Discussion of Relativistic Wave Equations, 211.
Basidiomycetes, antibiotics from (Anchel, Hervey, Kavanagh, Polatnick and Robbins), 498.
BEALE, G. H. Process of Transformation of Antigenic Type in *Paramecium Aurelia*, Variety 4, 418.
BELLMAN, R. On the Average Value of Arithmetic Functions, 149.
BELLMAN, R., and HARRIS, T. E. On the Theory of Age-Dependent Stochastic Branching Processes, 601.
Bernoulli numbers (Vandiver), 103.
Binaries, eclipsing (Sen), 311.
Biochemical mutants of *Neurospora* (Lein, Mitchell and Houlahan), 435.
Biochemistry of *Tetrahymena* (Kidder and Dewey), 566.
Black-eyed Susan (Stephens and Blakeslee), 252.
BLAKESLEE, A. F. See Stephens, S. G., 252.
BLUMEL, J., and KIRBY, H. Amino Acid Constituents of Tissues and Isolated Chromosomes of *Drosophila*, 561.
BLUMENTHAL, G. See Mazia, D., 328.
BOAS, R. P., JR. Exponential Transforms and Appell Polynomials, 481.
Body, chemical composition (Sherman and Ragan), 384.
BONNER, D. The Identification of a Natural Precursor of Nicotinic Acid, 5.
Boundaries of ULC sets (Newman), 193.
BROMAN, A. Conformal Mapping and Convergence of a Power Series, 605.
BUCHDAHL, H. A. A Special Class of Solutions of the Equations of the Gravitational Field Arising from Certain Gauge-Invariant Action Principles, 66.
BUERGER, M. J. Some Relations Between the F's and F^2's of X-Ray Diffraction, 277.
BURKHOLDER, P. R. See Sanders, M. E., 516.

CAMERON, J. W., and TEAS, H. J. The Relation Between Nicotinic Acid and Carbohydrates in a Series of Maize Endosperm Genotypes, 390.
CARSON, H. L., and STALKER, H. D. Reproductive Diapause in *Drosophila Robusta*, 124.
CASPARI, E., and RICHARDS, J. On the Proteins of a^+a^+ and *aa* Ephestia, 587.
CASTLE, W. E., and KING, H. D. Linkage Studies of the Rat, IX. Cataract, 135.
Cataract in rat (Castle and King), 135.
Categories (MacLane), 263.
CHANEY, R. W. The Bearing of the Living Metasequoia on Problems of Tertiary Paleobotany, 503.
Chromosome alterations in maize (Anderson), 387.
Chromosomes, amino acid in (Blumel and Kirby), 561.
Chromosomes, volutin on (Lindegren), 187.
CLARK, J. B. See Stone, W. S., 142.

Closed surfaces (Hopf), 47.
Conformal mapping (Broman), 605.
CONGER, A. D. The Cytogenetic Effect of Sonic Energy Applied Simultaneously with X-Rays, 470.
Congruences (Vandiver), 103.
Congruences, line (Kulk), 9.
Conjugate points (Hopf), 47.
Convergence of power series (Broman), 605.
Convexity (Salem and Zygmund), 443.
Convolution transforms (Hirschman and Widder), 152; (Schoenberg), 164.
COOPER, K. W. A New Theory of Secondary Non-disjunction in Female *Drosophila Melanogaster*, 179.
Coprinus similis (Anchel, Hervey, Kavanagh, Polatnick and Robbins), 498.
Critical points (Walsh), 111, 267.
Crossing over, suppression of (Dobzhansky and Epling), 137.
Curvature of matrices (Michal), 17.
Curves, physical families of (Kasner and De Cicco), 68, 169.
Cyclotomy (Vandiver), 62, 196.
Cytochemistry of Feulgen reaction (Di Stefano), 75.
Cytogenetic effect of sonic energy and X-rays (Conger), 470.

Datura embryos in culture (Sanders and Burkholder), 516.
Decay of isotropic turbulence (Lin), 540.
DE CICCO, J. See Kasner, E., 68, 169.
DEWEY, V. C. See Kidder, G. W., 81, 561.
Diapause (Carson and Stalker), 124.
Diet, protein and riboflavin in (Sherman and Ragan), 384.
Dietary enrichments (Sherman and Pearson), 585.
Dietary factors (Kidder and Dewey), 81.
Differential equation (Levinson), 13.
Differential equations of slip flow (Truesdell), 342.
Differential equations, stability of (Wallach), 203.
Differential matrices (Michal), 17.
Diffraction, X-ray (Buerger), 277.
DI STEFANO, H. S. A Cytochemical Study of the Feulgen Nucleal Reaction, 75.
DOBZHANSKY, T., and EPLING, C. The Suppression of Crossing Over in Inversion Heterozygotes of *Drosophila Pseudoobscura*, 137.
Drosophila, salivary gland (Kodani), 131.
Drosophila melanogaster (Cooper), 179; (Goldschmidt), 245.
Drosophila pseudoobscura (Dobzhansky and Epling), 137.
Drosophila robusta (Carson and Stalker), 124.
Drosophila virilis (Blumel and Kirby), 561.
Duality (MacLane), 263.
DUFRENOY, J. See Pratt, R., 323.

EBERLEIN, W. F. Abstract Ergodic Theorems, 43.
Eigenvalues, approximation of (Aronszajn), 474, 594.
EMERSON, S. A Physiological Basis for Some Suppressor Mutations and Possibly for One Gene Heterosis, 72.
Endosperm genotypes in maize (Cameron and Teas), 390.
Entire function (Marden), 405.
Enzymatic fixation of CO_2 (Ajl and Werkman), 491.
Enzyme-substrate films (Mazia and Blumenthal), 328.
Ephestia, proteins (Caspari and Richards), 587.
EPLING, C. See Dobzhansky, T., 137.
Equilibrium in a field (Walsh), 111.
Ergodic theorems (Eberlein), 43.
Errata (Evans), 347; (Uhler), 490.
Escherichia coli (Haas, Wyss and Stone), 229.
EVANS, G. C. Errata, 347.
EVERETT, C. J., and ULAM, S. Multiplicative Systems, I, 403.
Exponential sums (Weil), 204.
EYRING, H., FREDRICKSON, J. W., and MCLACHLAN, D., JR. The Mechanism of Flow for Solid Metals, 293.

Factorials, exact (Uhler), 407, 490.
FANKHAUSER, G., and GODWIN, D. The Cytological Mechanism of the Triploidy-Inducing Effect of Heat on Eggs of the Newt, *Triturus Viridescens*, 544.
FEDERER, H. Essential Multiplicity and Lebesgue Area, 611.
Fertilization in maize (Roman), 36.
Feulgen reaction (Di Stefano), 75.
Field, equations in finite (Vandiver), 62, 196; (Hua and Vandiver), 258.
FINE, N. J. Some New Results on Partitions, 616.
Flow in Metals (Eyring, Fredrickson, and McLachlan), 295.
Flow, Stability of (Pekeris), 285.
FREDERICKSON, J. W. See Eyring, H., 293.
Frequency functions of stellar velocities (Kiewiet de Jonge), 553.
Frequency of mutants (Stone, Haas, Clark and Wyss), 142.
Fungi, inhibitor of growth of (Pratt, Sah, Dufrenoy and Pickering), 323.

Galactic studies (Shapley), 27; (Shapley and Nail), 173.
GARSON, W., and WAKSMAN, S. A. Strain Specificity and Production of Antibiotic Substances, VIII. Production of a Grisein-like Antibiotic by a Strain of *Streptomyces Griseus*, 232.
Gas, flow of (Neményi and Prim), 119.

Gas spheres, polytropic (Kopal), 377.
Gas turbine (Soderberg), 239.
Gauge-invariants (Buchdahl), 66.
Generalized force fields (Kasner and De Cicco), 169.
Germany, tuberculosis in (Long), 271.
GODWIN, D. See Fankhauser, G., 544.
GOLDSCHMIDT, R. B. New Facts on Sex Determination in *Drosophila melanogaster*, 245.
Gravitational field (Buchdahl), 66.
Grisein-like antibiotic (Garson and Waksman), 232.
Group, representation of (Maatner), 52.
Groups, categories and duality (MacLane), 263.
Growth and amino acids (Sanders and Burkholder), 516.
Growth cessation and aging (Lansing), 304.
GUIRARD, B. M. See Wagner, R. P., 398.

HAAS, F., WYSS, O., and STONE, W. S. The Effect of Irradiation on Recombination in *Escherichia Coli*, 229.
HAAS, F. See Stone, W. S., 142.
Harmonic functions (Walsh), 111, 267.
HARRIS, T. E. See Bellman, R., 601.
Heat, triploidy-inducing (Fankhauser and Godwin), 544.
Hereditary antigenic differences (Sonneborn), 413.
HERSHEY, A. D., and ROTMAN, R. Linkage Among Genes Controlling Inhibition of Lysis in a Bacterial Virus, 89.
HERVEY, A. See Anchel, M., 498.
Heterosis, one gene (Emerson), 72.
HIRSCHMAN, I. I., JR., and WIDDER, D. V. An Inversion and Representation Theory for Convolution Transforms with Totally Positive Kernels, 152.
Homocystine utilization (Kidder and Dewey), 81.
Homotopy groups (Whitehead), 207.
HOULAHAN, M. B., and MITCHELL, H. K. Evidence for an Interrelation in the Metabolism of Lysine, Arginine and Pyrimidines in *Neurospora*, 465.
HOPF, E. Closed Surfaces without Conjugate Points, 47.
HOULAHAN, M. B. See Lein, J., 435.
HUA, L. K., and VANDIVER, H. S. On the Existence of Solutions of Certain Equations in a Finite Field, 258.
Hydroxyanthranilic acid (Mitchell and Nye), 1; (Bonner), 5.

Illumination and stereoscopic acuity (Mueller and Lloyd), 223.
Integral operators (Schoenberg), 164.
Integration (Stone), 336, 447, 483.
Inversion and representation of transforms (Hirschman and Widder), 152.
Inversion heterozygotes (Dobzhansky and Epling), 137.
Irradiation and recombination (Haas, Wyss and Stone), 229.

KASNER, E., and DE CICCO, J. Physical Families of Curves in Space, 68.
——. Physical Curves in Generalized Fields of Force, 169.
KAVANAGH, F. See Anchel, M., 498.
KIDDER, G. W., and DEWEY, V. C. Dietary Factors in the Utilization of Homocystine, 81.
——. Studies on the Biochemistry of *Tetrahymena*, XIV. The Activity of Natural Purines and Pyrimidines, 566.
KIEWIET DE JONGE, J. H. On the Relationships Between the Frequency Functions of Stellar Velocities, 553.
KING, H. D. See Castle, W. E., 135.
KIRBY, H. See Blumel, J., 561.
KODANI, M. The Protein of the Salivary Gland Secretion in *Drosophila*, 131.
KOPAL, Z. Radial Oscillations of the Limiting Models of Polytropic Gas Spheres, 377.
Koroyanitu, ascent of (Smith), 579.
KULK, W. V. D. On Line Congruences, 9.

Lacunary trigonometric series (Salem and Zygmund), 54.
LANSING, A. I. Evidence for Aging as a Consequence of Growth Cessation, 304.
Laplace transforms (Mackey), 156.
Leaf arrangement (Morley), 574.
Least squares (Piotrowski), 23.
Lebesgue area (Federer), 611.
LEIN, J., MITCHELL, H. K., and HOULAHAN, M. B. A Method for Selection of Biochemical Mutants of *Neurospora*, 435.
Lentinus degener (Anchel, Hervey, Kavanagh, Polatnick and Robbins), 498.
LEVINSON, N. A Simple Second Order Differential Equation with Singular Motions, 13.
LIN, C. C. Note on the Law of Decay of Isotropic Turbulence, 540.
LINDEGREN, C. C. The Origin of Volutin on the Chromosomes, Its Transfer to the Nucleolus, and Suggestions Concerning the Significance of This Phenomenon, 187.
Line congruences (Kulk), 9.
Linkage and bacterial virus (Hershey and Rotman), 89.
Linkage in the rat (Castle and King), 135.
LLOYD, V. V. See Mueller, C. G., 223.
LONG, E. R. Tuberculosis in Germany, 271.
Loop nebula (Shapley and Nail), 173.

Lysine metabolism (Houlahan and Mitchell), 465.

McCONAGHIE, V. M., and NIELSEN, H. H. Some Preliminary Results on the Spectra of AsH_3, AsD_3 and PH_3, 455.
MACKEY, G. W. The Laplace Transform for Locally Compact Abelian Groups, 156.
McLACHLAN, D., JR. See Eyring, H., 293.
MACLANE, S. Groups, Categories and Duality, 263.
Magellanic Clouds (Shapley), 27.
Maize, fertilization in (Roman), 36.
Maize, mutations in (Anderson), 387; endosperm genotypes (Cameron and Teas), 390.
MARDEN, M. The Number of Zeros of a Polynomial in a Circle, 15.
——. On the Zeros of the Derivative of an Entire Function of Finite Genre, 405.
Matrices with constant curvature (Michal), 17.
MAUTNER, F. I. The Completeness of the Irreducible Unitary Representations of a Locally Compact Group, 52.
MAZIA, D., and BLUMENTHAL, G. Inactivation of Enzyme-Substrate Films by Small Doses of X-Rays, 328.
Mersenne's numbers (Uhler), 102.
Metabolism of lysine, arginine and pyrimidines (Houlahan and Mitchell), 465.
Metals, flow in (Eyring, Fredrickson and McLachlan), 293.
Metasequoia glyptostroboides (Morley), 574
Metasequoia, living (Chaney), 503.
MICHAL, A. D. Infinite Dimensional Differential Matrices with Constant Curvature, 17.
Microörganisms grown on irradiated substrate (Stone, Haas, Clark and Wyss), 142.
Minimax (Shiffman), 96.
MITCHELL, H. K., and NYE, J. F. Hydroxyanthranilic Acid as a Precursor of Nicotinic Acid in *Neurospora*, 1.
MITCHELL, H. K. See Lein, J., 435; Houlahan, M. B., 465.
MORLEY, T. On Leaf Arrangement in *Metasequoia glyptostroboides*, 574.
Multiplicity, essential (Federer), 611.
MUELLER, C. G., and LLOYD, V. V. Stereoscopic Acuity for Various Levels of Illumination, 223.
Multiplicative systems (Everett and Ulam), 403.
Mutants, nutritional (Ryan), 425; biochemical (Lein, Mitchell and Houlahan), 435; predictable (Witkus), 442.
Mutation and selection among microörganisms (Stone, Haas, Clarke and Wyss), 142.
Mutations in maize (Anderson), 387.

NAIL, V. M. See Shapley, H., 173.
NATIONAL ACADEMY OF SCIENCES ORGANIZATION, 349–376. Officers, 349; Council, 349; Members, 349; Members Emeriti, 366; Foreign Associates, 367; Sections, 369; Committees, 373; Trust Funds, 374.
NEMÉNYI, P., and PRIM, R. Some Properties of Rotational Flow of a Perfect Gas, 119.
Neurospora, biochemical mutants (Lein, Mitchell and Houlahan), 435; metabolism of lysine (Houlahan and Mitchell), 465.
Neurospora, precursor of nicotinic acid in (Mitchell and Nyc), 1; (Bonner), 5.
Neurospora, reaction with synthesis of pantothenic acid (Wagner and Guirard), 398.
Neurospora, "sulfonamide - requiring" (Zalokar), 32.
NEWMAN, M. H. A. Boundaries of ULC Sets in Euclidean n-Space, 193.
Newt, *Triturus viridescens* (Fankhauser and Godwin), 544.
Nicotinic acid (Mitchell and Nyc), 1; (Bonner), 5.
Nicotinic acid and carbohydrates in maize (Cameron and Teas), 390.
NIELSEN, H. H. See McConoghie, V. M., 455.
Non-disjunction in *Drosophila* (Cooper), 179.
Nucleolus, transfer of volutin to (Lindegren), 187.
Nutritional life history (Sherman and Pearson), 585.
Nutritional mutants (Ryan), 425.
NYC, J. F. See Mitchell, H. K., 1.

Operators (Aronszajn), 474, 594.

Paleobotany, tertiary (Chaney), 503.
p-Aminobenzoic acid and *Neurospora* (Zalokar), 32.
Pantothenic acid (Wagner and Guirard), 398.
Paramecium (Sonneborn), 413; (Beale), 418.
Partitions (Fine), 616.
PEARSON, C. S. See Sherman, H. C., 585.
PEKERIS, C. L. Stability of the Laminar Flow Through a Straight Pipe of Circular Cross-Section to Infinitesimal Disturbances Which Are Symmetrical about the Axis of the Pipe, 285.
Physical curves (Kasner and De Cicco), 68, 169
Physiological Basis for suppressor mutations and one gene heterosis (Emerson), 72.
PICKERING, V. L. See Pratt, R., 323.

Pigments of yellow-eyed races of *Rudbeckia hirta* (Stephens and Blakeslee), 252.
PIOTROWSKI, S. L. Some Remarks on the Weights of Unknowns as Determined by the Method of Differential Corrections, 23.
Pipe, flow in (Pekeris), 285.
POLATNICK, J. See Anchel, M., 498.
Polynomials, zeros of (Marden), 15; Appell (Boas), 481
Power series (Broman), 605.
PRATT, R., SAH, P. T., DUFRENOY, J., and PICKERING, V. L. Vitamin K_3 as an Inhibitor of the Growth of Fungi and of Fermentation by Yeast, 323.
Precursor of nicotinic acid (Mitchell and Nyc), 1; (Bonner), 5.
PRICE, W. H. The Stimulatory Action of Certain Fractions from Bacteria and Yeast on the Formation of Bacterial Virus, 317.
PRIM, R. See Neményi, P., 119.
Prime mover (Soderberg), 239.
Protein in diet (Sherman and Ragan), 384.
Protein of salivary secretion (Kodani), 131.
Proteins of Ephestia (Caspari and Richards), 587.
Pulse index for variable stars (Shapley), 27.
Purines and pyrimidines (Kidder and Dewey), 566.
Pyrimidines, metabolism (Houlahan and Mitchell), 465.

Radial oscillations of gas spheres (Kopal), 377.
RAGAN, M. S. See Sherman, H. C., 384.
Random number of random variables (Robbins), 162.
Rat, cataract in (Castle and King), 135.
Rayleigh-Ritz and A. Weinstein approximations of eigenvalues (Aronszajn) 474, 594.
Recombination in *Escherichia coli* (Haas, Wyss and Stone), 229.
Reflection effect in binaries (Sen), 311.
Relativistic wave equations (Bargmann and Wigner), 211.
Representations of a locally compact group (Mautner), 52.
Reproductive diapause (Carson and Stalker), 124.
Riboflavin in diet (Sherman and Ragan), 384.
RICHARDS, J. See Caspari, E., 587.
ROBBINS, H. On the Asymptotic Distribution of the Sum of a Random Number of Random Variables, 162.
ROBBINS, W. J. See Anchel, M., 498.
ROMAN, H. Directed Fertilization in Maize, 36.
Rotational flow (Neményi and Prim), 119.
ROTMAN, R. See Hershey, A. D., 89.
Rudbeckia hirta (Stephens and Blakeslee), 252.
RYAN, F. J. On the Stability of Nutritional Mutants of Bacteria, 425.

SAH, P. T. See Pratt, R., 323.
SALEM, R., and ZYGMUND, A. On Lacunary Trigonometric Series, II, 54.
——. A Convexity Theorem, 443.
Salivary gland (Kodani), 131.
SANDERS, M. E., and BURKHOLDER, P. R. Influence of Amino Acids on Growth of Datura Embryos in Culture, 516.
SCHOENBERG, I. J. On Variation-Diminishing Integral Operators of the Convolution Type, 164.
SEN, H. K. Reflection Effect in Eclipsing Binaries for a Point-Source of Light, 311.
Sex determination (Goldschmidt), 245.
SHAPLEY, H. Galactic and Extragalactic Studies, XVIII. The Pulse Index for Eighty-Nine Variable Stars in the Magellanic Clouds, 27.
SHAPLEY, H., and NAIL, V. M. Galactic and Extragalactic Studies, XIX. Giant Variable Stars of the Loop Nebula (30 Doradus), 173.
SHERMAN, H. C., and PEARSON, C. S. Nutritional Life History as Influenced by Dietary Enrichments, III. Full-Life Data of 1946–1948 Experiments, 585.
SHERMAN, H. C., and RAGAN, M. S. Effects of Different Protein and Riboflavin Contents of Diet upon the Chemical Composition of the Body, 382.
SHIFFMAN, M. A Theory of Minimax, 96.
Shock waves (Thomas), 526.
Singular motion (Levinson), 13.
Slip flow (Truesdell), 342.
SMITH, A. C. An Ascent of Koroyanitu, 579.
SODERBERG, C. R. The Gas Turbine and Its Significance as a Prime Mover, 239.
Sonic energy, cytogenetic effect (Conger), 470.
SONNEBORN, T. M. The Determination of Hereditary Antigenic Differences in Genically Identical *Paramecium* Cells, 413.
Spaces with vanishing groups (Whitehead), 207.
Spectra of AsH_3, AsD_3 and PH_3 (McConaghie and Nielsen), 455.
Stability of differential equations (Wallach), 203.
Stability of laminar flow (Pekeris), 285.
Stability of shock waves (Thomas), 526.
STALKER, H. D. See Carson, H. L., 124.
Statistical theory of turbulence (von Kármán), 530.

Stellar velocities (Kiewiet de Jonge), 553.
STEPHENS, S. G., and BLAKESLEE, A. F. Pigments of Yellow-Eyed Races of the Black-Eyed Susan (*Rudbeckia Hirta*), 252.
Stereoscopic acuity (Mueller and Lloyd), 223.
Stochastic processes (Bellman and Harris), 601.
STONE, M. H. Notes on Integration, I, 336; II, 447; III, 483.
STONE, W. S., HAAS, F., CLARK, J. B., and WYSS, O. The Role of Mutation and of Selection in the Frequency of Mutants Among Microörganisms Grown on Irradiated Substrate, 142.
STONE, W. S. See Haas, F., 229.
Strain specificity (Garson and Waksman), 232.
Streptomyces griseus (Garson and Waksman), 232.
Sums, exponential (Weil), 204.
Suppression of crossing over (Dobzhansky and Epling), 137.
Suppressor mutations (Emerson), 72.
Surfaces, closed (Hopf), 47.
Symmetry and critical points (Walsh), 267.
Synthesis of pantothenic acid (Wagner and Guirard), 398.

TEAS, H. J. See Cameron, J. W., 390.
Tetrahymena, biochemistry (Kidder and Dewey), 566.
THOMAS, T. Y. On the Stability and Instability of Shock Waves, 526.
Tissues, amino acid in (Blumel and Kirby), 561.
Transformation of antigenic type (Beale), 418.
Transforms (Hirschman and Widder), 152; (Mackey), 156.
Trigonometric series (Salem and Zygmund), 54.
Trinomial equations (Vandiver), 196.
Triploidy-inducing effect of heat (Fankhauser and Godwin), 544.
Triturus viridescens (Fankhauser and Godwin), 544.
TRUESDELL, C. On the Differential Equations of Slip Flow, 342.
Tuberculosis in Germany (Long), 271.
Turbulence (von Kármán), 530; (Lin), 540.

UHLER, H. S. On All of Mersenne's Numbers, Particularly M_{193}, 102.
——. Twenty Exact Factorials Between 304! and 401!, 407, 490.
ULAM, S. See Everett, C. J., 403.
ULC sets (Newman), 193.

VANDIVER, H. S. Applications of Cyclotomy to the Theory of Nonhomogeneous Equations in a Finite Field, 62.
——. New Types of Congruences Involving Bernoulli Numbers and Fermat's Quotient, 103.
——. Cyclotomic Power Characters and Trinomial Equations in a Finite Field, 196.
VANDIVER, H. S. See Hua, L. K., 258.
Variable stars (Shapley), 27; (Shapley and Nail), 173.
Virus, bacterial (Hershey and Rotman), 89; (Price), 317.
Vitamin K_1 (Pratt, Sah, Dufrenoy and Pickering), 323.
Volutin, origin of (Lindegren), 187.
VON KÁRMÁN, T. Progress in the Statistical Theory of Turbulence, 530.

WAGNER, R. P., and GUIRARD, B. M. A Gene-Controlled Reaction in *Neurospora* Involving the Synthesis of Pantothenic Acid, 398.
WAKSMAN, S. A. See Garson, W., 232.
WALLACH, S. The Stability of Differential Equations with Periodic Coefficients, 203.
WALSH, J. L. Critical Points of Harmonic Functions as Positions of Equilibrium in a Field of Force, 111.
——. Methods of Symmetry and Critical Points of Harmonic Functions, 267.
Wave equations, relativistic (Bargemann and Wigner), 211.
Weights of unknowns (Piotrowski), 23.
WEIL, A. On Some Exponential Sums, 204.
WERKMAN, C. H. See Ajl, S. J., 491.
WHITEHEAD, G. W. On Spaces with Vanishing Low-Dimensional Homotopy Groups, 207.
WIDDER, D. V. See Hirschman, I. I., Jr., 152.
WIGNER, E. P. See Bargmann, V., 211.
WITKUS, E. R. A Predictable Mutation in Bacteria, 442.
Wyss, O. See Stone, W. S., 142.
——. See Haas, F., 229.

X-ray diffraction (Buerger), 277.
X-rays, cytogenetic effect (Conger), 470.
X-rays, inactivation by (Mazia and Blumenthal), 328.

Yeast, actions of fractions (Price), 317; inhibitor of (Pratt, Sah, Dufrenoy and Pickering), 323.

ZALOKAR, M. The *p*-Aminobenzoic Acid Requirement of the "Sulfonamide-Requiring." Mutant Strain of *Neurospora*, 32.
Zeros of polynomial (Marden), 15; of derivative of entire function (Marden), 405.
ZYGMUND, A. See Salem, R., 54, 443.